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Sampling Ground-dwelling Ants: Case Studies from the World's Rain Forests

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and Ted Schultz



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Contents

Addresses of authors and contributors	v
Foreword	ix
Chapter 1 Litter ant communities of the Brazilian Atlantic rain forest region	1
Chapter 2 Ants species diversity in the Western Ghats, India	19
Chapter 3 Investigation of the diversity of leaf-litter inhabiting ants in Pasoh, Malaysia	31
Chapter 4 Ant inventories along elevational gradients in tropical wet forests in Eastern Madagascar	41
Chapter 5 The Australian rain forest ant fauna: A biogeographic overview	51
Chapter 6 Ground ant communities from central Amazonia forest fragments	59
Chapter 7 Minesite rehabilitation studies: A method for visualizing succession	71

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Foreword

The assessment of biological resources at a given time and given location is the basis of most conservation decisions. However, due to the lack of standardised survey protocols, the results can rarely contribute to the monitoring of biological resources over time, nor to comparisons over space (UNEP 1995).

Biodiversity is a complex matter. No one single group of organisms can indicate the wealth of all the diversity at a given site. At the same time, it is impossible to survey all the organisms at a given site. One approach to overcoming this problem is to choose to survey those groups of organisms that are ecologically important, relatively easily collected in a standardized way, reasonably diverse at a given site, identifiable, and for which an acceptable level of scientific knowledge is at hand, both in the form of publications and available experts. Ants, particularly ground-dwelling ants, are the perfect match for such an approach.

The use of ants in conservation and biodiversity research was the subject of symposia at the International Conference of the International Union for the Study of Social Insects (IUSI) in Paris in 1995. The study of ant diversity was also proposed as a new approach to conservation from within the Social Insects Specialists Group of the Species Survival Commission of the World Conservation Union (SSC/IUCN). The positive and stimulating response from these groups led finally to the organization of the ALL (Ants of the Leaf Litter) conference on the use of ants in biodiversity studies.

In August 1996, 24 scientists from around the world met in a wonderful surrounding in Ilhéus in Bahia's Atlantic rain forest in Brazil. Each one was invited to elaborate on a specific topic related to the broad overall question of whether, and how, tools might be developed to bring ants into the focus of biodiversity and conservation research. After a week of lively discussions, we all agreed that ants could effectively serve as such a tool, and a standard protocol was born. The standard protocol, the ALL Protocol, is about to be published in a manual entitled 'Ants: Standard Methods for Measuring and Monitoring Biodiversity' (Agosti et al. in press).

Our focus on ground-dwelling ants is based on the uniqueness of this fauna and the specific, tested methods by which it can be surveyed. Adequate methods for the standardized sampling of ants in the canopy and on vegetation have not been developed. Because of this lack of quantitative methods, we felt that a wider focus that included these non-ground-dwelling ant faunas would weaken the strength of the protocol and prohibit the collection of comparative data.

The vitality of the proposed standard protocol is shown through its growing application on all continents. The protocol has mainly been developed in tropical and subtropical areas and works best in those areas. The decreasing diversity of ants correlated with increasing proximity to the Arctic and Antarctic regions sets limits on its application in some northern and southern regions. The increased aridity in some regions sets yet another limit. Preliminary results, however, show that sifting leaf litter in savanna ecosystems is still possible and yields interesting results. Other methods explained in the manual add more information on surveys in such areas.

We originally intended to publish a series of case studies in the manual. However, on reflection, it was decided that these would be better presented in a companion volume in order to document the type of faunas that might be encountered, highlight some of the logistic problems that can occur, and demonstrate the sort of data that can be generated from such studies. This is the volume.

The papers in this issue have been selected to provide supplementary information on the ant faunas of rain forests in various regions of the world. They include chapters on the Atlantic rain forest in Brazil (Chapter 1), the Western Ghats in India (Chapter 2), a forest reserve in Malaysia (Chapter 3), various localities in Madagascar (Chapter 4) and temperate and tropical rain forest throughout Australia (Chapter 5). The information in these chapters highlights some of the features that future scientists should expect to encounter when surveying ant faunas in these regions.

It should be stressed that these studies were carried out prior to, or during, the period when the ALL Standard Protocol was being evaluated. Consequently, although some of the studies use elements of the protocol, others are more

idiosyncratic in their approach. The Australian rain forest Chapter draws upon a range of surveys that have used different sampling methodologies and intensities. This has created limitations on the generalities that may be inferred across studies, but nevertheless provides a lesson in how to reduce data to the lowest common denominator so that comparisons can be made.

One additional chapter illustrates how elements of the sampling protocol can be used to investigate the effects of fragmentation in Amazon rain forest in northern Brazil (Chapter 6). Finally, a short Chapter on African and Brazilian mine site rehabilitation (Chapter 7) illustrates how multivariate ordination-type procedures can be used to visualize succession in areas that are undergoing restoration.

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Chapter 1 - Litter ant communities of the Brazilian Atlantic rain forest region

Jacques H. C. Delabie, Donat Agosti and Ivan C do Nascimento

Introduction

Atlantic rain forest once occupied about one million square kilometers of the eastern part of Brazil, extending from Rio Grande do Norte to Rio Grande do Sul in a strip ranging from several km to 160 km wide. Along with some parts of Amazonia, it probably exhibits the highest rate of endemism of the biota in Brazil. Considerable tracts of Atlantic rain forest have been cleared as a result of several waves of exploitation, so much so that its loss is considered to be more severe than that of any other forest types in South America (Mori et al. 1983). At the national level, less than 8.8 percent of this ecosystem remains (Câmara 1991), and much of it that still exists is represented in small fragments and linear strips of vegetation (Fonseca 1985). The site of this study (the southern portion of Bahia) is representative of the northern section of the Atlantic rain forest.

Cocoa, *Theobroma cacao*, was introduced from Amazonia to this region during the 18th century. Many cocoa plantations are traditionally grown under retained native trees to provide the necessary shade for the plantation (Delabie 1990) and this provides a habitat which retains many features of the original Atlantic rain forest, including that of the litter ant fauna (Delabie et al. 1994; Delabie and Fowler 1995). Because of this, the cocoa economy has resulted in the preservation of a component of the native fauna and flora, and a consideration of the cocoa ant fauna tells us much about that of the original Atlantic rain forest.

In the past 15 years, the Bahia region has undergone major changes due to the erosion of the cocoa economy. Many cocoa plantations have been seriously damaged by the accidental introduction of witch's broom disease, caused by the fungus *Crinipellis perniciosa*, and there has been a steady decline in the world market for cocoa. As a result, many cocoa plantations have been abandoned (Alger and Caldas 1996). The death of the cocoa trees has

resulted in many plantations being replaced by open fields, often for raising cattle. These changes result in habitat that is considerably drier, with consequent modification of the native ant communities. These changes in land use are similar to those in the cocoa region of Trinidad that occurred 50 years ago (Strickland 1945) and they may ultimately lead to larger scale changes in the indigenous flora and fauna.

The aim of this study is to analyze and inventory the ant fauna of this region before much of it is lost. We first describe the results of an extensive series of data obtained from Winkler sack samples of litter. This litter was taken from a plot within an old cocoa plantation which has not been treated with any pesticides for many years. In earlier papers, the community structure of the soil and litter ant fauna (extracted by Berlese funnels) of the same area has been described (Delabie and Fowler 1993, 1995; Fowler and Delabie 1995). Here, we present information about the species which have been found and the structure of the community, and this is then augmented with information obtained from other areas of the region. Following this, information on the cocoa plantation ants and these additional species is integrated in order to propose a general scheme for placing them into guilds, based on their habitat preferences and roles in the ecosystem.

Methods

Field work was carried out in the cocoa experimental areas of the Center for Cocoa Research (CEPLAC), Itabuna, Bahia (14° 45'S, 39° 13'W).

Five hundred samples of leaf litter were taken between January and May, 1996, in a 0.87 hectare area situated in an old cocoa plantation (about 60 years old), where pesticides had not been used for at least 30 years. One square meter samples of litter were sieved in the field and placed in Winkler sacks in the laboratory for 24 hours. The resulting ant data were then expressed as percentage frequency of occurrence in the 500 samples, and then an analysis of the positive and negative associations between species was made using the same methods used for studies of arboreal ant mosaics, namely χ^2 analysis with Yates' correction applied (Room 1971; Majer et al. 1994). The nomenclature conforms to Bolton (1995).

Results

The fauna

The number of ants found in the 1m² samples in the cocoa plantation varied considerably; most of the samples yielded between 5 and 12 species, with an average number of 8.05 species per sample (Figure 1). That is much more than the previously published figure (< 6 species) derived from Berlese funnel sampling (Delabie and Fowler 1995).

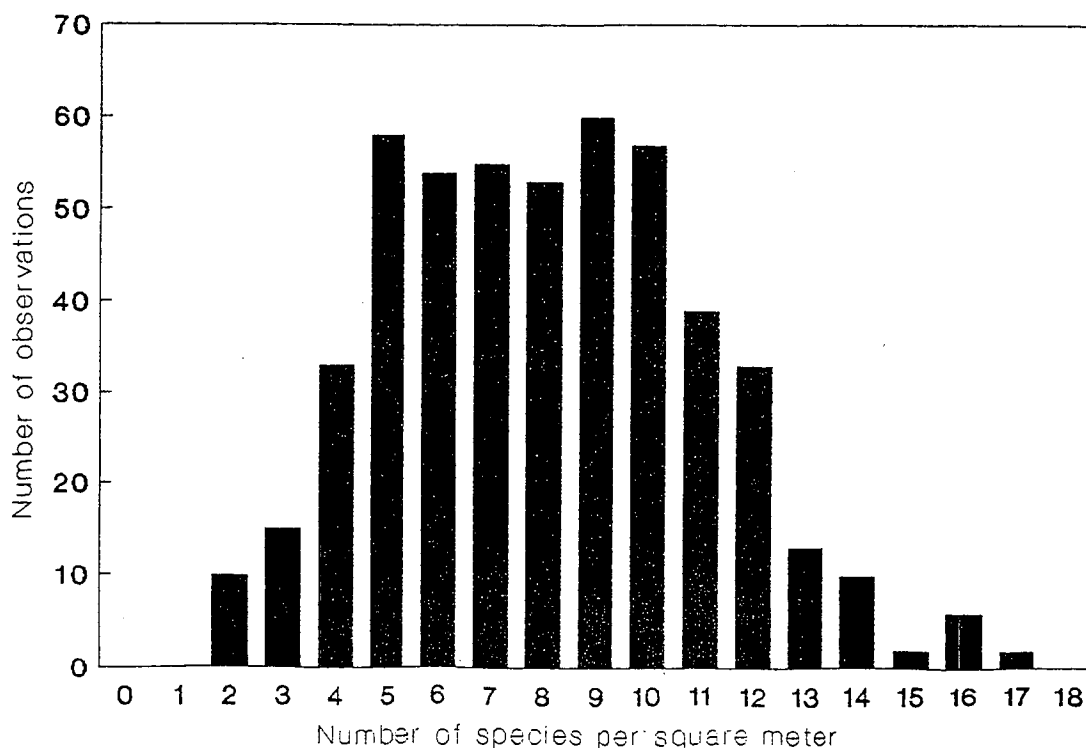


Figure 1. Distribution of the number of ant species per sample in 500 Winkler sack samples taken in a cocoa plantation in southern Bahia, Brazil.

The 106 ant species sampled by the Winkler sacks are listed in Table 1, which also shows their relative frequency in the 500 samples. *Solenopsis* sp. 47 exhibits a strong numerical dominance, being present in 75% of the samples. Several species are present in more than one quarter of the samples, amongst which are found generalist predators (*Hypoponera* sp.3, *Odontomachus meinerti*), specialist predators (*Octostruma stenognatha*, *O. balzani*), specialized Homoptera-tending species (*Acropyga decedens*, *A. berwicki*), a

fungus-growing species (*Mycocepurus smithii*) and various omnivores (*Solenopsis* spp., *Pheidole* sp.3, *Paratrechina* sp.1). Other common species (present in >10% of the samples) include generalist predators (*Hypoponera* sp.2, *Gnamptogenys moelleri*, *Odontomachus haematodus*), many omnivorous genera (*Brachymyrmex*, *Camponotus*, *Crematogaster*, *Paratrechina*, *Pheidole*, *Tapinoma*) and fungus-growing species (*Sericomyrmex bondari*, *Cyphomyrmex rimosus*).

The 106 species are from 43 genera belonging to 7 subfamilies as follows: Cerapachyinae - 1 genus, 1 species; Dolichoderinae - 3 genera, 4 species; Ecitoninae - 2 genera, 3 species; Formicinae - 4 genera, 12 species; Myrmicinae - 23 genera, 59 species; Ponerinae - 10 genera, 26 species; and Pseudomyrmecinae - 1 genus, 1 species. The most speciose genus is *Pheidole* (10 spp), followed by *Gnamptogenys* (7), *Crematogaster* (6), *Strumigenys* (6), *Apterostigma* (5), *Pachycondyla* (5) and *Paratrechina* (5).

Most of the species can be considered as characteristic of the litter layer, where they nest and forage. This is the case, for example, with the Cerapachyinae, all the Ponerinae (with the exception of the arboreal *Pachycondyla constricta*), Myrmicinae of the tribes Attini (*Apterostigma*, *Cyphomyrmex*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex*, *Trachymyrmex*), Basicerotini (*Octostruma*, *Rhopalothrix*), Dacetoniini (*Glamyromyrmex*, *Gymnomyrmex*, *Neostruma*, *Strumigenys*), and species belonging to the genera *Brachymyrmex*, *Hylomyrma*, *Megalomyrmex*, *Oligomyrmex*, *Rogeria*, *Solenopsis* and *Stegomyrmex*, plus miscellaneous species such as *Dolichoderus imitator*. Some species are also found on the vegetation; examples include most of the *Crematogaster* and *Paratrechina* species, and also *Camponotus cingulatus* (see Delabie et al. 1991a).

Little information is available on the biology of most of these ants. Within the Ponerinae, *Leptogenys* are thought to be predators of terrestrial crustaceans (Fowler et al. 1991) and *Thaumatomyrmex* spp. are predators of millipedes (Brandão et al. 1991). Most of the other Ponerinae seem to be generalist predators, although observations on *Gnamptogenys* indicate that *G. annulata* may be a predator of termites (J. H. C. Delabie unpub. data.), *G. horni* is an ant predator (Hölldobler and Wilson 1990) and *G. minuta* preys on millipedes (Brandão and Lattke 1990).

Table 1. Relative frequency of ant species obtained in 500 Winkler sack samples in a cocoa plantation in southern Bahia, Brazil.

Species	Percent	Species	Percent
Cerapachyinae		Myrmicinae	
<i>Cerapachys splendens</i>	0.6	<i>Apterostigma</i> sp.1	8.6
Ponerinae		<i>Apterostigma</i> sp.2	0.8
<i>Amblyopone elongata</i>	0.4	<i>Apterostigma</i> sp.3	1.6
<i>Anochetus bispinosus</i>	7.2	<i>Apterostigma</i> sp.4	0.2
<i>Anochetus mayri</i>	4.6	<i>Apterostigma</i> sp.5	0.8
<i>Ectatomma permagnum</i>	0.8	<i>Crematogaster acuta</i>	4.0
<i>Gnamptogenys annulata</i>	0.4	<i>Crematogaster evallans</i>	12.4
<i>Gnamptogenys horni</i>	0.8	<i>Crematogaster limata</i>	13.2
<i>Gnamptogenys minuta</i>	0.2	<i>Crematogaster quadriformis</i>	0.4
<i>Gnamptogenys moelleri</i>	12.6	<i>Crematogaster</i> sp.1	3.6
<i>Gnamptogenys rastrata</i>	1.2	<i>Crematogaster</i> sp.3	0.2
<i>Gnamptogenys sp. nr. horni</i>	9.2	<i>Cyphomyrmex peltatus</i>	6.4
<i>Hypoponera</i> sp.1	3.4	<i>Cyphomyrmex rimosus</i>	11.2
<i>Hypoponera</i> sp.2	21.4	<i>Glamyromyrmex appretiatus</i>	1.6
<i>Hypoponera</i> sp.3	47.8	<i>Gymnomyrmex rugithorax</i>	2.8
<i>Leptogenys crudelis</i>	0.2	<i>Hylomyrma sagax</i>	3.0
<i>Leptogenys dasygyna</i>	0.4	<i>Hylomyrma</i> sp.1	1.0
<i>Odontomachus haematodus</i>	11.6	<i>Leptothorax tristani</i>	0.2
<i>Odontomachus meinerti</i>	29.6	<i>Megalomyrmex</i> sp.	0.4
<i>Pachycondyla bucki</i>	0.8	<i>Megalomyrmex sylvestrii</i>	1.0
<i>Pachycondyla constricta</i>	0.2	<i>Mycocepurus smithii</i>	38.0
<i>Pachycondyla harpax</i>	3.2	<i>Myrmicocrypta buenzlii</i>	2.0
<i>Pachycondyla stigma</i>	0.6	<i>Neostruma</i> sp.	1.8
<i>Pachycondyla venusta</i>	0.8	<i>Octostruma balzani</i>	29.4
<i>Thaumatomyrmex atrox</i>	1.0	<i>Octostruma jheringhi</i>	5.2
<i>Thaumatomyrmex contumax</i>	0.6	<i>Octostruma stenognatha</i>	33.4
<i>Typhlomyrmex pusillus</i>	0.2	<i>Octostuma rugifera</i>	7.4
Pseudomyrmecinae		<i>Oligomyrmex panamensis</i>	4.2
<i>Pseudomyrmex tenuis</i>	0.6	<i>Oligomyrmex</i> sp.	0.4
Ecitoninae		<i>Pheidole</i> sp.1	13.2
<i>Labidus coecus</i>	1.6	<i>Pheidole</i> sp.10	1.0
<i>Labidus praedator</i>	0.4	<i>Pheidole</i> sp.15	0.8
<i>Neivamyrmex gibbatus</i>	0.2	<i>Pheidole</i> sp.2	0.4
Dolichoderinae		<i>Pheidole</i> sp.3	29.0
<i>Azteca paraensis bondari</i>	4.4	<i>Pheidole</i> sp.5	4.8
<i>Dolichoderus imitator</i>	2.6	<i>Pheidole</i> sp.6	8.6
<i>Dolichoderus lutosus</i>	0.4	<i>Pheidole</i> sp.7	6.2
<i>Tapinoma melanocephalum</i>	20.8	<i>Pheidole</i> sp.8	1.2
Formicinae		<i>Pheidole</i> sp.9	0.2
<i>Acropyga berwicki</i>	25.0	<i>Rhopalothrix</i> sp.	0.6
<i>Acropyga decedens</i>	45.2	<i>Rogeria besucheti</i>	1.2
<i>Brachymyrmex heeri</i>	24.6	<i>Rogeria scobinata</i>	3.2
<i>Camponotus cingulatus</i>	23.8	<i>Rogeria</i> sp.	3.0
<i>Camponotus crassus</i>	0.4	<i>Rogeria subarmata</i>	0.4
<i>Camponotus novogranadensis</i>	2.2	<i>Sericomyrmex bondari</i>	24
<i>Camponotus trapezoides</i>	0.4	<i>Solenopsis</i> sp.145	7.6
<i>Paratrechina fulva</i>	3.2	<i>Solenopsis</i> sp.47	75.0
<i>Paratrechina longicornis</i>	4.8	<i>Solenopsis</i> sp.1	38.8
<i>Paratrechina</i> sp.1	28.6	<i>Stegomyrmex vizottoi</i>	1.2
<i>Paratrechina</i> sp.2	20.6	<i>Strumigenys carinithorax</i>	3.2
<i>Paratrechina</i> sp.3	2.4	<i>Strumigenys denticulata</i>	7.6
		<i>Strumigenys elongata</i>	1.8
		<i>Strumigenys louisianae</i>	0.2
		<i>Strumigenys perparva</i>	0.4
		<i>Strumigenys</i> sp.1	0.6
		<i>Trachymyrmex cornetzi</i>	2.6
		<i>Trachymyrmex relictus</i>	1.0
		<i>Tranopelta gilva</i>	0.8
		<i>Wasmannia auropunctata</i>	8.4

Within the Formicinae it is surprising to encounter the very high frequency of two species of *Acropyga* in the Winkler sack samples when compared to the samples in the same area extracted with Berlese funnels a few years ago (Delabie and Fowler 1995). The presence of these ants has already been observed in the soil layer, where they are abundant, but it was thought that they were not so common in the litter (Delabie and Fowler 1995). This new series of data shows that their apparent absence was an artifact, probably due to the extraction mode of the Berlese funnels; these ants may not move through the litter in the funnels, or, more probably, they are unable to withstand any dehydration in the heated funnels (J. H. C. Delabie unpublished data).

Within the Myrmicinae, the Attini present were less evolved members of the tribe (*Apterostigma*, *Cyphomyrmex*, *Mycocepurus*, *Myrmicocrypta*), except perhaps *Trachymyrmex*. These ants are reported as using insect carcasses and faeces, or dead plant material, to rear their symbiotic fungi in order to gain nutrition (Weber 1972). The Basicerotini are generally considered to be predators (Brown and Kempf 1960), while no information is available on *Octostruma* spp. The Dacetoniini are known to be specialist predators of Collembola (Hölldobler and Wilson 1990), but nothing is known about the biology of highly specialized genera, such as *Glamyromyrmex*, *Gymnomyrmex* and *Neostruma*. There is also no information available on the activities of *Rogeria* in the litter layer (Kugler 1994). *Stegomyrmex vizottoi* acts as a myriapod egg predator (Diniz and Brandão 1993) and *Oligomyrmex* preys on eggs of several groups of arthropods (Hölldobler and Wilson 1990).

Amongst the other ants, *Paratrechina* spp. and *Crematogaster* spp., as well as *Camponotus cingulatus*, are omnivorous and generally tend homopterans on the trees for their honeydew. The foraging on the floor can be a seasonal phenomenon, possibly associated with low production of honeydew during dry periods, such as during this sampling period.

The common *Wasmannia auropunctata* deserves particular attention, since it is considered to be a typical species of forest litter which, under conditions of ecological perturbation, can be a very successful colonizer of new habitats, including urban areas. It is also abundant on trees where it tends mealybugs (Delabie 1988, 1990). It has

been suggested that *Tranopelta gilva* is a predator or competitor of *Acropyga* spp. (Delabie and Fowler 1993), although there is no confirmation of its interaction with these ants. The interdependence of *T. gilva* and *Acropyga* spp. in the soil layer (Delabie and Fowler 1993) has not been verified in the current study since *T. gilva* was very uncommon in the litter, while *Acropyga decedens* was much more frequent than initially expected (Delabie and Fowler 1995). *Acropyga* spp. tend mealybugs on the superficial roots of the cocoa trees and other plants of the cocoa plantations (Delabie 1990; Delabie and Fowler 1990, 1993, 1995; Delabie et al. 1991b; Encarnação et al. 1993).

Some species (e.g., *Pachycondyla constricta*, as already said, and also *Azteca paraensis bondari*, *Dolichoderus lutosus*, *Camponotus* spp. (excluding *C. cingulatus*) and *Leptothorax tristani*) are primarily arboreal and are only incidentally found in the litter layer. Some army-ants (Ecitoninae) were occasionally collected, and their action as generalist predators in the litter layer can influence the composition of the fauna. However, they are only rarely found at a given site due to their nomadic life-style, so their influence tends to be ephemeral. *Pseudomyrmex tenuis* is one of the rare soil-nesting species of this genus and is usually found in open areas such as pastures and the sea-shore. Its presence in the plantation is probably linked to openings in the cocoa canopy.

The mosaic of leaf-litter ants

Previous studies have indicated that, both in the Old and New World Tropics, arboreal ants are distributed in a three dimensional mosaic in which dominant ant species form mutually exclusive blocks, each with their own suite of sub-dominant and non-dominant ants (Room 1971; Majer et al. 1994). Figure 2 shows the significant positive and negative associations ($P < 0.05$) between members of the cocoa leaf litter ant community. The number of associations provides strong evidence of a mosaic in this stratum as well, although in terms of the strata in which the interacting ants occur, its structure is radically different from the other arboreal mosaics already studied (cf.

Figure 2 with diagrams in Room 1971 and Majer et al. 1994). In this cocoa plantation, four species exhibit one to seven positive associations (some are true cryptic ants), and four species (none are cryptic) are only associated with the rest of the community via negative associations. There are at least two types of negative associations: a) competition for niche space (e.g., amongst members of the ground-dwelling genera *Octostruma*, *Acropyga* and *Odontomachus*); and b) interactions with arboreal species (e.g., *Pheidole* sp.75, *Crematogaster limata*, *Camponotus cingulatus* and *Odontomachus haematodus*). The arboreal species are frequently found in suspended soil (associated with epiphytes), where they are often more abundant than on the forest floor. An exception is *O. haematodus*, which is as frequent on the ground as in suspended soils. When present on the ground these ants exclude the true soil and litter species, and thus act as dominant or subdominant species. This effect is possibly seasonal.

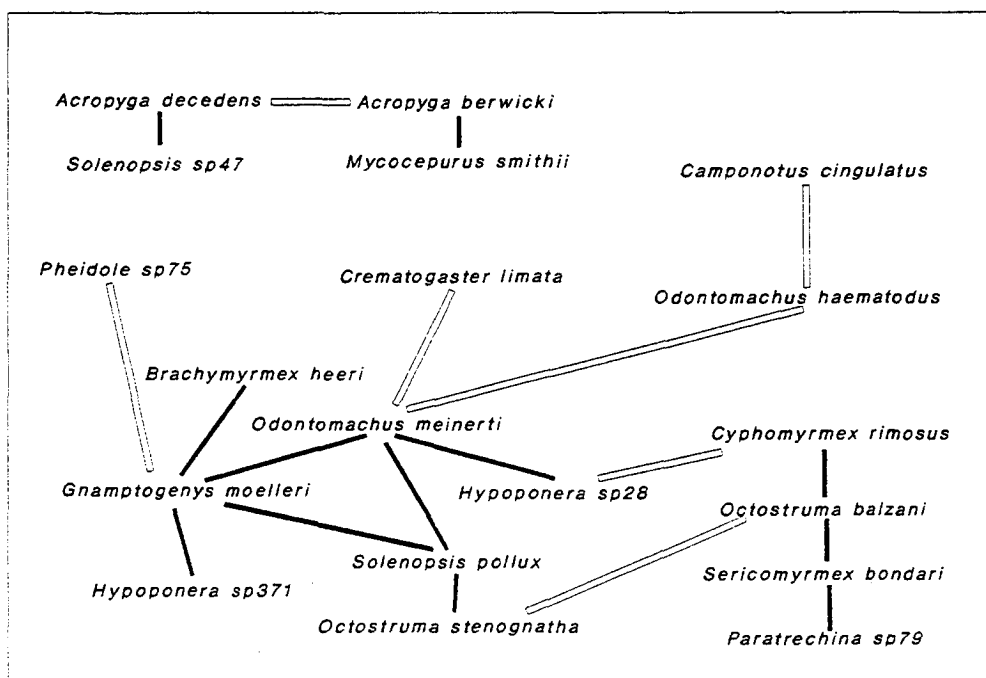


Figure 2. Mosaic structure of leaf-litter ants in a cocoa plantation, southern Bahia, Brazil. Solid and open lines respectively indicate significant ($P < 0.05$) positive and negative associations.

In summary, the mosaic which exists in the litter layer results from the interactions of two groups of ants of different origins, the first comprising ground-dwelling species, generally with a cryptic behaviour and which generally interact with each other, and the second group, consisting of a few arboreal species, which probably forage on the floor during unfavorable conditions on the trees and interact with the ground ant fauna. The second group can dominate the ground-dwelling species, and has a considerable influence on the composition of the ant community at the base of trees. At greater distances from tree bases the ant community is more characteristic of the purely ground-dwelling ant community.

Other relevant information on leaf-litter ants in southern Bahia.

Additional species are found in other localities of the region (in cocoa plantations or secondary and primary forests) and deserve special mention. These are discussed below within their subfamilies.

Within the Ponerinae, *Simopelta minima* has been collected on two occasions by other methods used to sample the soil and litter of the same plantation described in this chapter (see Brandão 1989; Delabie and Fowler 1995). Ants of this genus have an army ant-like behavior, exhibiting mass recruitment and are probably nomadic (Gotwald and Brown 1966). Other genera of Cerapachyinae and Ponerinae which are occasionally found in the litter layer of Bahia include possible egg-predators (e.g., *Discothyrea sexarticulata* and *Proceratium brasiliense*), isopod-predators (e.g., *Leptogenys* spp.), myriapod-predators (e.g., *Amblyopone* spp., *Prionopelta* sp., *Thaumatomyrmex contumax* and *T. atrox*), termite-predators (e.g., *Acanthostichus* sp. and *Cylindromyrmex brasiliensis*) or ant-predators (e.g., *Cerapachys splendens* and *Gnamptogenys horni*).

Few Pseudomyrmecinae are found on the ground, except *Pseudomyrmex tenuis* and *P. termitarius* which nest in the soil and are commonly found in degraded lands. Both can sometimes be found in shaded areas, such as in cocoa plantations. The only

species in this genus which nests in rotten wood on the ground is *P. kuenckeli*, but there is no information about its ecology.

We have little information on the species of Ecitoninae which live in Bahia. *Neivamyrmex* has approximately 10 species in the region, and several species hunt other ants. Males are often caught at light traps, but the workers of only three species are occasionally found. Most of them have a cryptic life-style and build galleries, as does another genus of ant-hunting Ecitoninae, *Nomamyrmex*.

Although not found in the survey reported here, the higher genera of Attini are common in the Atlantic rain forest of southern Bahia, including cocoa plantations. Included here are *Atta cephalotes* and *Acromyrmex subterraneus brunneus*, which nest superficially in the ground. Nests of the latter are largely covered by pieces of cut leaves, which consequently look like the litter.

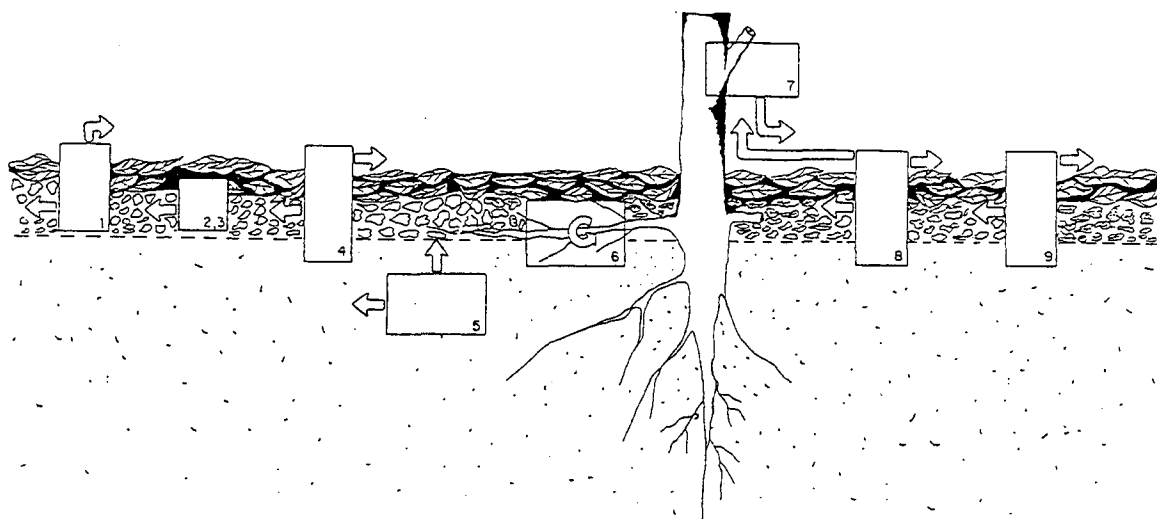
An introduction to the South American soil ant guilds

Little information is available on the community organization of the South American soil ants. However, from our experience of studying soil ants of the Atlantic rain forest region, it is now possible to make a first attempt at delimiting ants into guilds based on their foraging, feeding and nesting characteristics. Most of the inferences presented here are probably also true for a range of rain forest types from the neotropical region.

Nine categories of guilds are distinguished (Figure 3). With the exception of few cases, the ants are considered at the generic level as there is a reasonable degree of communality of foraging or nesting habits amongst different species of a genus. The position of some genera is tentative and in such instances they are indicated by a ? symbol. The bibliographic references, when already cited in the last paragraphs, are not repeated.

Guild 1: Litter omnivores and scavengers - This guild includes some of the most speciose genera (e.g., *Pheidole*, although the foraging and nesting strategies of most of

these species remains completely unknown) and some species with high population densities (e.g., *Solenopsis*, sub-genus *Diplorhoptrum*). We also place in this guild *Megalomyrmex* and the cryptic *Blepharidatta*, *Lachnomyrmex* (?), *Octostruma* (?) and *Rogeria* (?), although no information is available about their foraging strategies.



Key to ants guilds of the soil and litter layers in the Atlantic rain forest, southern Bahia

1. **Litter omnivores and scavengers** (cryptic or otherwise): *Blepharidatta*, *Lachnomyrmex*?, *Megalomyrmex*, *Pheidole*, *Octostruma*?, *Solenopsis*, *Rogeria*?
2. **Specialist litter predators** (cryptic): *Acanthostichus*, *Amblyopone*, *Cerapachys*, *Cylindromyrmex*, *Discothyrea*, *Eurhopalothrix*, *Gnamptogenys* (few species), *Leptogenys*, *Hylomyrma*?, *Octostruma*?, *Oligomyrmex*, *Proceratium*, *Prionopelta*, *Rhopalothrix*?, *Stegomyrmex*, *Thaumatomyrmex*, *Typhlomyrmex*, *Dacetoniini* (*Glamyromyrmex*, *Gymnomyrmex*, *Neostruma*, *Smithistruma*, *Strumigenys*).
3. **Litter generalist predators** (cryptic or otherwise): *Hypoponera*, *Gnamptogenys* (most of the species), *Anochetus*.
4. **Army ants and army-ant like species** (cryptic or otherwise, generalist or specialist predators): *Ecitoninae* (*Eciton*, *Labidus*, *Neivamyrmex*, *Nomamyrmex*), *Simopelta*.
5. **Soil cryptic predators**: *Pachycondyla holmgreni*, *Tranopelta*?, *Centromyrmex* (exclusively in termite (*Syntermes* spp.) nests).
6. **Subterranean mealybug-dependent species** (cryptic): *Acropyga*, *Tranopelta*?
7. **Omnivorous arboreal-nesting dominants, incidentally or seasonally foraging on the floor and in the litter**: *Azteca*, *Crematogaster*.
8. **Soil or litter dominants, also foraging on the vegetation, the ground or the litter**: A - Generalist predators: *Odontomachus*, *Ectatomma*; B - Omnivores: *Brachomyrmex*, *Camponotus*, *Monomorium*, *Paratrechina*, *Solenopsis*, *Wasmannia*.
9. **Soil or litter nesting fungus-growers**: Several genera of *Attini*, such as *Acromyrmex*, *Apterostigma*, *Atta*, *Cyphomyrmex*, *Mycocrepus*, *Myrmicocrypta*, *Sericomyrmex*, *Trachymyrmex*, which use arthropod refuse, dead or live plant material.

Figure 3. Guild organization of leaf-litter ants in the Atlantic rain forest region, southern Bahia, Brazil.

Guild 2. Litter specialist predators - We place in this guild a range of cryptic species on the basis of their behaviour and foraging characteristics. These are *Acanthostichus*, *Amblyopone*, *Cerapachys*, *Discothyrea*, *Eurhopalothrix*, *Leptogenys*, *Hylomyrma* (?), *Octostruma* (?), *Oligomyrmex*, *Proceratium*, *Prionopelta*, *Rhopalothrix* (?), *Stegomyrmex*, *Thaumatomyrmex*, *Typhlomyrmex*, some highly specialized species of *Gnamptogenys* (*alfaria* group), and several Dacetonini, including *Glamyromyrmex*, *Gymnomyrmex*, *Neostruma*, *Smithistruma* and *Strumigenys*.

Guild 3. Litter generalist predators - This category includes the different species of *Hypoponera* and *Anochetus*, which are generally cryptic, and most of the species of *Gnamptogenys*.

Guild 4. Army ants and army ant-like species - This guild includes all the Ecitoninae, whether cryptic or not, namely *Eciton*, *Labidus*, *Neivamyrmex* and *Nomamyrmex*, and also the ponerine genus *Simopelta*.

Guild 5. Soil cryptic predators - We place in this category a few species which are rarely found (but common in certain places) and which are exclusively cryptic. Included is *Tranopelta* (?) (but see next guild) and *Pachycondyla* (formerly *Wadeura*) *holmgreni* which, because of its strong morphological convergence with *Centromyrmex*, is probably a termite predator; it is exclusively found in *Syntermes* nests (Delabie 1995).

Guild 6. Subterranean mealybug-dependent species - We put in this category the common, but extremely cryptic, *Acropyga* and possibly the problematic *Tranopelta* (?). The first-mentioned has a mutualistic association with highly specialized mealybugs of the tribe Rhizoecini which are found on the roots of various plant species.

Guild 7. Omnivorous arboreal nesting dominants foraging on the floor - The occurrence on the floor of some species of dominant *Crematogaster* and *Azteca* can result from a permanent or seasonal extension of their territory. As already mentioned, they exert a strong influence on the soil-dwelling species as a result of predation and/or food resource competition.

Guild 8. Soil or litter dominants - These ants forage on vegetation, on the forest floor or in the litter. We subdivide this category in two groups: a) large generalist predators, such as *Odontomachus* and *Ectatomma* (some species of these genera also forage on vegetation looking for nectar); and b) true omnivores such as *Brachymyrmex*, *Camponotus*, *Monomorium*, *Paratrechina*, *Solenopsis* (larger species), and *Wasmannia*.

Guild 9. Soil and litter nesting fungus-growers - This guild consists of members of the Attini, including the genera *Acromyrmex*, *Apterostigma*, *Atta*, *Cyphomyrmex*, *Mycocrepus*, *Myrmecocrypta*, *Sericomyrmex* and *Trachymyrmex*, which use arthropod refuse and carcasses and/or dead or live plant material to cultivate their symbiotic fungus.

Conclusions

Even if we draw on the published information about ants living in the leaf-litter of Bahia, it is of concern that we still know relatively little about the ecology and behaviour of most of the resident species. In addition, information on the degree of endemism and the geographic distribution of many species is inadequate and continues to be updated. We know which species are probably true endemics (such as a remarkable new species of *Blepharidatta* and also *Simopelta minima*) but, because many species are litter-living, cryptic organisms, they have never been satisfactorily sampled in the Neotropics, so their endemism could well be overestimated. Due to the ecological similarities with the Amazonian region and also the climatic variations

which occurred during the early quaternary (Ab'Saber 1977), the northern part of the Atlantic rain forest has previously been in contact with the Amazonia rain forest. There are many cases of species, arboreal as well as soil-living, which have their populations divided in two large zones, one in each of the major forest types. One of the more classical examples is *Atta cephalotes*, but we could also cite examples from different genera, such as *Anochetus*, *Hylomyrma*, *Ochetomyrmex* and *Pachycondyla*.

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Chapter 2 - Ants species diversity in the Western Ghats, India

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Introduction

There are very few long-term studies of tropical insect species diversity. This may in part be attributed to lack of economic development of most tropical countries, the lack of adequate facilities for research, and sometimes to the lack of tradition in modern scientific work. However, we felt that, at least sometimes, this is due to the lack of appropriate research methodology suitable for tropical countries. We therefore developed a standardized package of methods for quantitative sampling of insects by tropical ecologists with modest research budgets. This methodology combines the use of a small, locally fabricated, battery-operated light trap as well as vegetation sweeps, pitfall traps and scented traps. We have used this package of methods to sample insect species diversity patterns in several areas of India.

During this study, we encountered 16,852 adult insects belonging to 1789 species, 219 families and 19 orders. Application of a variety of statistical analyses suggested that this package of methods is adequate for reliably sampling insects and for differentiating habitats on the basis of the distribution of insect species (Gadagkar et al. 1990).

Encouraged by the success of this package of methods for insects as a whole, we then focused our attention more specifically on ants, with the dual aims of documenting ant diversity patterns and exploring the possibility of using ants as indicators of biodiversity (Gadagkar et al. 1993).

Materials and methods

Study Sites

Our study sites were located in the Uttara Kannada district of the state of Karnataka, India. The forested study sites fall broadly into two categories reflecting different levels of

disturbance, namely, the "Reserve Forests" (R.F.) (relatively less disturbed) and the "Minor Forests" (M.F.) (relatively more disturbed). Sites representing both categories were chosen in the coastal plains, as well as at higher elevations (approximate altitude 600 m). Sites were selected to ensure that they represented different habitats and levels of disturbance. In addition to these forested habitats, three monoculture plantations (PL.) and a forest which was regularly harvested to produce leaf manure (Betta land) were also chosen for study. At each of these sites, sampling was carried out in three one hectare plots. Thus a total of 36 one hectare plots from 12 habitat types were sampled. A brief description of each study site is given in Table 1. The study was carried out during December, January, February and March 1983-5, which is part of the dry season in these localities.

Sampling methods

Four trapping methods were employed:

- (1) Light trap - A portable light trap which can be easily assembled and dismantled was fabricated using locally-available inexpensive materials. The light trap uses a 10 inch fluorescent light source (Eveready Fluorolite; 6 Watts) powered by 1.5 Volt battery cells. The main framework of the trap consists of four iron legs, an aluminium roof and two aluminium baffles, between which the light source is placed. Insects attracted to the light were collected through a funnel in a cyanide jar, below the light. One light trap was placed in the centre of the plot. The light was switched on at dusk and allowed to burn itself out as the batteries drained after about seven hours. The insects trapped in the jar were collected the next morning and preserved in 70% alcohol.
- (2) Vegetation Sweeps - Sweeps were carried out to collect insects off vegetation. The nets were made of thick cotton cloth with a diameter of 30 cm at the mouth and a bag length of 60 cm. The plot was divided into 100 quadrats, measuring 10m x 10m each. Six such quadrats were chosen at random and the entire ground level vegetation was swept with the net. Sweeps were always done between 1000 h - 1200 h.

Table 1. A brief description of study sites

Sites	Vegetation type	Dominant tree species	Remarks
Santagal R.F.	Evergreen	<i>Cinnamomum</i> , <i>Bischofia</i> and <i>Diospyros</i> spp.	Thick tree canopy, understorey of Cane breaks.
Nagur R.F	Evergreen	<i>Holigarna</i> and <i>Hopea</i> spp.	Thick tree canopy, understorey of saplings.
Mirjan M.F.	Scrub	<i>Ixora</i> , <i>Buchnanian</i> and <i>Terminalia</i>	Highly degraded semi-evergreen.
Chandavar M.F.	Semi-evergreen	<i>Ixora</i> , <i>Aporosa</i> and <i>Hopea</i> spp.	Degraded, understorey of frequently lopped saplings.
Bengle M.F.	Moist deciduous	<i>Terminalia</i> spp.	Degraded, thick under- growth of grass and annual herbs.
Bidaralli R.F.	Moist deciduous	<i>Terminalia</i> , <i>Xylia</i> and <i>Lagerstromia</i> spp.	Undergrowth of herbs and shrubs, mainly <i>Clerodendrum</i> .
Sonda R.F.	Moist deciduous	<i>Terminalia</i> , <i>Xylia</i> and <i>Aporosa</i>	Understorey mainly of <i>Psychotria</i> spp.
Bhairumbe M.F.	Moist deciduous	<i>Caryea</i> , <i>Ziziphus</i> and <i>Randia</i>	Degraded, undergrowth of <i>Chromelina</i> .
Betta land	Moist deciduous	<i>Terminalia</i> and <i>Lagerstromia</i>	Cleared of all undergrowth, maintained for leaf manure.
Eucalyptus Pl.	Monoculture	<i>Eucalyptus</i> spp.	Thick undergrowth of grass and herbs, surrounded by extensive moist-deciduous forest.
Teak Pl.	Monoculture	<i>Tectona grandis</i>	Little or no undergrowth except <i>Lantana</i> and <i>Chromelina</i> .
Areca Pl.	Monoculture	<i>Areca catechu</i>	Plantations in valleys, surrounded by evergreen forest on hills.

(3) Pitfall traps - These consisted of a 2.5 litre plastic jar with an opening of 9 cm in diameter, buried at ground level and protected from rain by a tripod stand carrying a plastic plate of about 30 cm diameter, situated 15 cm above the ground. One pitfall trap was placed in each of five randomly-chosen 10 m x 10 m quadrats. Each jar carried 25 ml of 0.05% methyl parathion. The traps were set up between 1500 h and 1700 h and were collected the next morning.

(4) Scented traps - A plastic jar of 2.5 litre capacity was used to fabricate a scented trap. The mouth of the jar was shielded from rain water using a plastic plate, with a gap of 6 cm between the mouth of the jar and the plate to enable insects to freely move into the jar. The trap was baited with 200 ml of saturated jaggery (unrefined cane sugar) solution with two tablets of baker's yeast, 0.05% methyl parathion emulsion and 0.5 ml of pineapple essence. The traps were hung at about 1 m from the ground on wooden pegs. Five such traps were used, one each in the centre of a randomly-chosen 10m x 10m quadrat. The scented traps were also set

between 1500 h and 1700 h and collected the following morning. Insects trapped in the solution were filtered, washed and preserved in 70% alcohol.

In addition to trapping insects by the methods described above, an intensive hand collection was made in each one hectare plot to collect representatives of as many species of ants as possible. Two persons made the search for one hour between 1400 h and 1500 h in every case. No attempt was made to estimate abundance by this method.

Data analysis

As an index of (within site) diversity, we computed ∞ of the log series (Fisher et al. 1943) by the equation:

$$S = \log_e (1 + N/\infty)$$

where S is the number of species in the sample, N is the number of individuals in the sample, and ∞ is the index of diversity. The standard deviation of ∞ was estimated as $\infty/\{-\log(1-X)\}$ where $X = N/(N + \infty)$ (Anscombe 1970). Using the standard deviation, significant differences in diversity between habitats were judged by the z test. This index is often recommended as a useful measure of within site diversity, even when the underlying distribution is not necessarily a log series (Krebs 1985).

β (between sites or between method) diversity was estimated as coefficients of similarity given by the Morishita-Horn index (Wolda 1981):

$$C = \frac{2\sum(n_{1i}n_{2i})}{(\lambda_1 + \lambda_2).N_1N_2}$$

$$\text{where } \lambda_j = \frac{\sum n_{ji}^2}{N_j^2}$$

and where n_{ji} is the number of individuals of species i in sample j and n_j is the number of individuals in sample j . The index was computed with data logarithmically transformed as $\ln(n_{ji} + 1)$. Cluster analysis was performed using a simple-linkage algorithm. Where only presence-absence data were available, such as with hand collecting, the Jaccard index was used to compute similarity (Ludwig and Reynolds 1988):

$$J_{AB} = \frac{a}{a + b + c}$$

where a = the no of species common to both sites, b = the no of species found only at A and c = the no of species found only at B.

Results and Discussion

This study provides the first estimates of ant diversity and abundance for any forest locality of India. Overall, we obtained 140 species of ants belonging to 32 genera and 6 sub-families in the 12 localities (Table 2). Each 3 ha locality yielded between 8 to 16 genera and 13 and 33 species (Table 3). Ants accounted for 5.4 - 12.8% of all insect species caught and 5.1 - 43.2% of all insect numbers caught in these localities (see Gadagkar et al. 1990, for data on other insect groups sampled in these plots). It is not easy to compare these numbers with other regions of the world because the number of studies is few and they have used different methods.

Comparison of trapping and hand collecting

The combination of the four trapping methods used was somewhat more successful than hand collecting, yielding 120 species from 31 genera while hand collecting yielded 101 species from 27 genera. More significant is the fact that the traps and hand collecting yielded different species; while 78 species were obtained by both methods, the traps yielded 42 unique species and hand collecting yielded 20 unique species. It appears therefore, that in spite of the efficacy of the traps, a combination of trapping and hand collecting may be desirable.

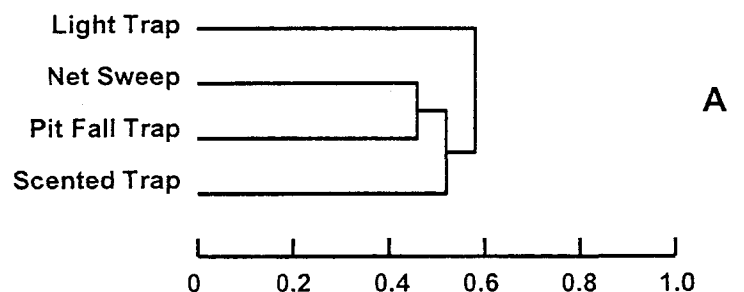
Of the four trapping methods used, pitfall traps sampled the most species, followed by vegetation sweeps, scented traps and light traps in that order. The fact that pitfall traps and vegetation sweeps were more successful is not surprising, indeed the fact that scented traps and light traps yielded as many ants as they did is surprising. Not only did the scented traps and light traps yield more ants than expected, they yielded an ant fauna rather different from that obtained by the other methods. The combination of several trapping methods that we have used is therefore of particular value (Figure 1).

Table 2. Summary of ant species collected from twelve localities in Western Ghats by a combination of quantitative sampling methods and hand collection.

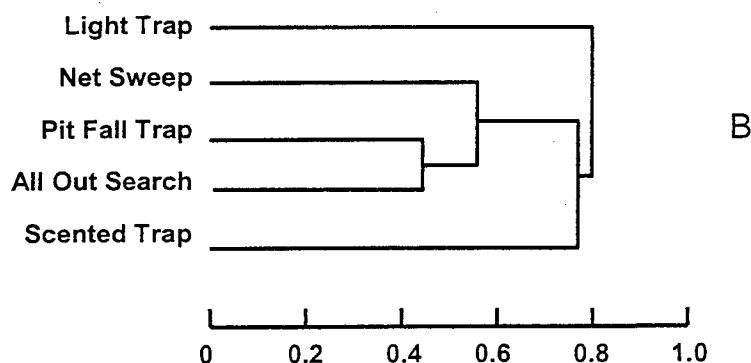
Subfamilies	Genera	Number of species
Ponerinae	<i>Diacamma</i>	1
	<i>Leptogenys</i>	2
	<i>Pachycondyla</i>	5
Aenictinae	<i>Aenictus</i>	2
Dorylinae	<i>Dorylus</i>	3
Pseudomyrmecinae	<i>Tetraponera</i>	3
Myrmicinae	<i>Aphaenogaster</i>	1
	<i>Cardiocondyla</i>	3
	<i>Cataulacus</i>	2
	<i>Crematogaster</i>	14
	<i>Rhoptiromyrmex</i>	2
	<i>Lophomyrmex</i>	2
	<i>Meranoplus</i>	2
	<i>Monomorium</i>	17
	<i>Myrmicaria</i>	1
	<i>Pheidole</i>	24
	<i>Pheidologeton</i>	3
	<i>Solenopsis</i>	1
	<i>Tetramorium</i>	5
	<i>Recurvidris</i>	1
Dolichoderinae	<i>Iridomyrmex</i>	1
	<i>Tapinoma</i>	9
	<i>Technomyrmex</i>	1
Formicinae	<i>Lepisiota</i>	4
	<i>Anoplolepis</i>	1
	<i>Camponotus</i>	12
	<i>Oecophylla</i>	1
	<i>Paratrechina</i>	2
	<i>Plagiolepis</i>	5
	<i>Polyrhachis</i>	6
	<i>Prenolepis</i>	4
TOTAL: 7	31	140

Table 3. Comparison of ant abundance and diversity in different localities

Locality	No.of subfamilies	No.of genera	No.of species	No.of individuals	Diversity index (∞ of log series)	% ant species among all insect species trapped	% ants among all insects trapped
Santagal	2	10	25	104	10.44	12.7	18.2
Nagur	5	15	32	159	12.07	21.2	21.9
Mirjan	5	16	27	149	9.64	12.6	5.1
Chandavar	5	16	30	118	12.98	12.8	7.0
Bengle	4	15	29	344	7.55	9.2	22.5
Bidaralli	3	16	33	423	8.37	10.0	32.4
Sonda	5	12	21	132	7.04	11.4	20.9
Bhairumbe	4	14	19	124	6.26	11.0	19.0
Betta	4	14	25	267	6.75	10.6	24.2
Eucalyptus	4	16	25	368	6.06	6.1	11.6
Teak	3	8	16	155	4.48	13.7	43.2
Areca	4	9	13	419	2.54	5.4	19.2



Distance = 1 - Morishita-Horn index



Distance = 1 - Jaccard index

Figure 1. Dendrograms comparing different sampling methods by ant species trapped. Data pooled from 36 plots for each sampling method. A, distance = 1 - Morishita - Horn index of similarity. B, distance = 1 - Jaccard index.

Comparison of localities based on ant fauna

The diversity of the ant fauna varied sufficiently between the 12 localities that several pairs of localities could be distinguished from each other by statistically comparing their levels of ant diversity (Table 4). This ability to discriminate between localities inspires confidence that our methodology is adequate and reproducible.

Although the preliminary nature and small sample sizes of this study preclude us from drawing any firm conclusions regarding the possible causes of variation in ant diversity between localities, two preliminary conclusions may be drawn. One is that relatively disturbed localities show relatively lower richness and diversity in their ant fauna than those which are less disturbed. This trend is evident in the monoculture plantations and the Betta land (Table 3). There is similar evidence in the literature for

Table 4. Comparison of localities in Western Ghats by their respective ant species diversity levels. Pairs of sites that are significantly different from each other in their levels of ant species diversity as measured by of the olog series. A "+" in any cell indicates that the site mentioned in the row is significantly more diverse than the site mentioned in the column ($p < 0.05$). Numerals (1) and (12) in row and column headings refer to different sites. The mean and standard deviation for each site are given in the row titles. Names of sites in row and column titles are ordered according to diversity.

		Site											
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
1.	Chandavar M.F. 12.98 ± 2.37						+	+	+	+	+	+	+
2.	Nagur R.F. 12.07 ± 2.13							+	+	+	+	+	+
3.	Santagal R.F. 10.44 ± 2.09											+	+
4.	Mirjan M.F. 9.64 ± 1.85											+	+
5.	Bidaralli R.F. 8.37 ± 1.46												+
6.	Bengle M.F. 7.55 ± 1.40												+
7.	Sonda R.F. 7.04 ± 1.54											+	+
8.	Betta Land 6.75 ± 1.35										+		+
9.	Bhairumbe M.F. 6.26 ± 1.43												+
10.	Eucalyptus PL 6.06 ± 1.21												+
11.	Teak PL 4.48 ± 1.12												
12.	Areca PL 2.54 ± 0.70												

reduction in ant diversity due to disturbance. For example, a significant reduction in ant species richness was found after slashing and burning of a tropical forest in Mexico (Mackey et al. 1991). The second conclusion is that there is a weak, but statistically significant, positive correlation between ant species diversity and plant species diversity (Figure 2). This is in contrast to an inverse correlation between bird species richness and plant species richness observed in the same general locality (Daniels et al. 1992). Note that plants and bird species diversity were simultaneously studied by our colleagues in the same localities at the same time (Bhat et al. 1986, 1987; Chandrashekara et al. 1984).

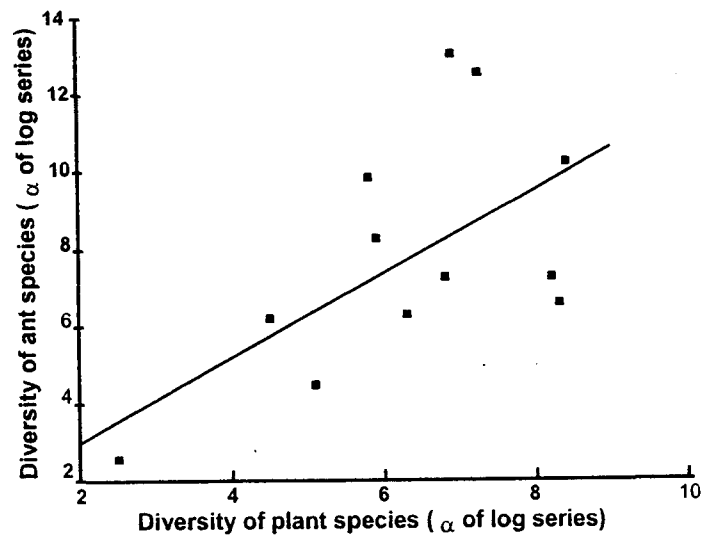


Figure 2. Scatter plot showing the relationship between plant and ant species diversity. For both ants and plants, diversity is measured by α of the log series. The fitted line is given by the equation $Y = 0.99 + 1.08X$. The slope is significantly greater than zero, $p < 0.02$. The relationship between ant and plant species diversity is also evident from a correlation analysis: Pearson product moment correlation = 0.63, $p < 0.05$; Kendall's rank correlation coefficient = 0.42, $p = 0.05$.

Comparison of the ant fauna sampled in different seasons in the two selected localities shows that seasonal variation within the locality is negligible when compared with variation between localities. This suggests that the ant fauna is highly locality specific. The tight clustering in the dendrograms of the ant fauna from different months within a locality, and the wide separation of the fauna between the two localities (Figure

3), inspires further confidence in the ability of our methods to adequately sample and thus permit comparison of habitats.

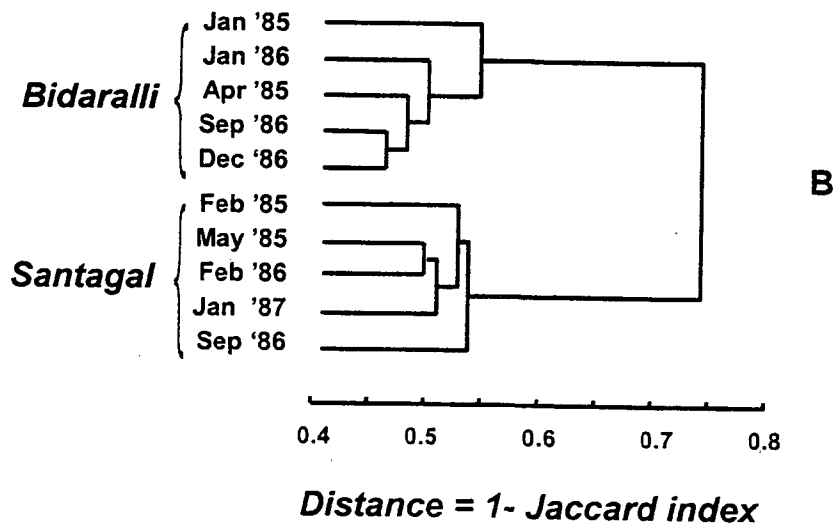
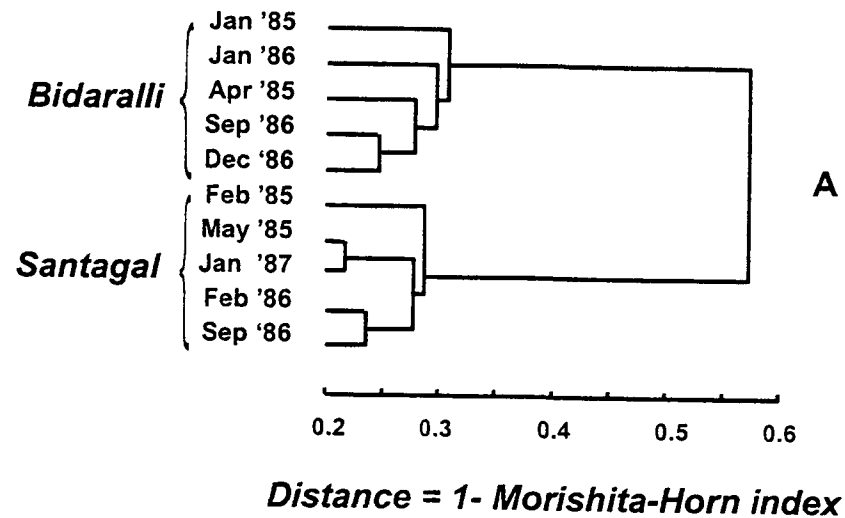


Figure 3. Dendrograms comparing ant fauna in different seasons sampled from two localities. Data pooled from six repeated samplings from a single one hectare plot for each season in each locality. A, distance = 1 - Morishita - Horn index of similarity. B, distance = 1 - Jaccard index.

In conclusion, although these studies are at a very preliminary stage, they suggest that the ant fauna of the Western Ghats is sufficiently rich to warrant more detailed

investigations on ant biodiversity, ecology and behaviour. There is also reasonable evidence that ants may be good candidates as indicator species for insect biodiversity in this region.

Acknowledgements

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Chapter 3 - Investigation of the diversity of leaf-litter inhabiting ants in Pasoh, Malaysia

Annette Malsch

Introduction

Malaysia, and the adjacent parts of Indonesia, are probably the largest truly ever-wet areas in the world (Richards 1978). The area is located in the great paleotropic region and reaches from South-East Asia to Northern Australia; it is also referred to as "The Malay Archipelago". The whole region is situated on two tectonic plates which are thought to have collided some 15 million years ago. This collision brought about an oceanic rift valley between Borneo and Sulawesi, which has enormous biological significance because it constitutes the boundaries of two floristic and faunistic regions: the Sunda Shelf (Malaysia, Philippines, Indonesia in part) and the Sahul Shelf (Indonesia in part, New Guinea, Northern Australia). Until today, both supercontinents have possessed their own characteristic flora and fauna, and this clearly-defined frontier is called the "Wallace-Line". The Malay Peninsula is dominated by an extremely species-rich dipterocarp lowland forest. It is the most extensive forest formation in Malaysia and has been comprehensively described by Aiken and Leigh (1992).

The aim of this investigation is to document the diversity and type of leaf-litter inhabiting ants of a representative Malaysian rain forest.

Methods

The Pasoh Forest Reserve

Of formerly 100,000 ha lowland rainforest on the Malay Peninsula, only 6000 ha are left today. The Pasoh Forest Reserve is situated in Negeri Sembilan, West Malaysia, about 140 kilometres south-east of Kuala Lumpur (2°59'N, 102°19'E) and is one of the last undisturbed

lowland rain forest areas. The centre of the reserve is a 650 ha primary lowland dipterocarp forest situated between 75 and 150 m above sea level. The Pasoh Forest Reserve is, in many respects, a typical example of a south-east Asian "ever-wet" lowland rain forest and has been subject to ecological research for many years.

The vegetation of this area is dominated by various species of *Shorea* and *Dipterocarpus*, both characteristic genera of this type of forest (Soepadmo 1978). Shaharuddin (1990) differentiates three main vertical strata in this type of forest: 1) the loose crown layer at 30 - 40 m height; 2) the continuous crown layer at 20 up to 25 m height; and, 3) beneath this, the third stratum with smaller trees and shrubs.

Pasoh receives a relatively low amount of annual rainfall, with 2000 mm on average, which is well distributed throughout the year (Shaharuddin 1990). The average temperature is 24°C and the relative humidity just above the soil (0-5 cm) is 98 % and exhibits little daily variation. Therefore a constant microclimate is experienced by the humus and leaf-litter level (Aoki et al. 1978).

Sampling design

A total of 9 plots (each 25 m²) were investigated. Each plot comprised a 5 x 5 m² area with an additional 3 x 3 m² area nested in the middle of the plot (Figure 1). Each of the two nested areas (16 m² and 9 m²) were sampled separately and the sum of the two equalled a 25 m² area. This provided the possibility of comparing all nested areas within plots and also the whole plots with each other.

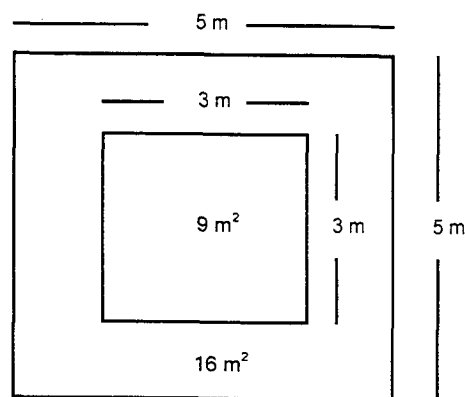


Figure 1. Nested sampling plot design

These plots were randomly selected 10 or more meters away from access trails, by the following criteria: 1) only moderate growth of shrubs and small trees for better accessibility and to be able to keep experimental disturbance to a minimum (e.g., to avoid bending or cutting off twigs and rattans); 2) more than 60 % overshadowing on the soil surface (estimated by open spaces of the canopy); 3) no permanent waterlogging of the soil; 4) an absence of large trees and logs or similar objects which would reduce the area available for sampling and, moreover, would alter the microhabitat in their vicinity (e.g., decomposing logs); and 5) more than 80% of ground covered with leaf-litter.

Before taking samples, the marked areas were given a minimum recovery phase of two days prior to sampling. In addition to this type of area-based sampling, collections were also performed on two decomposing logs and their immediate surroundings. Logs were selected from the immediate vicinity of the above mentioned plots. From each log, three samples were taken: 1) from the log itself; 2) from the thick humus layer at the border of the log; and 3) from the surrounding leaf-litter. These samples were only used for completing the faunistical overview.

Sampling of ants

Ants from the leaf-litter were extracted by Winkler sacks. Some special procedures that I followed should be explained. Firstly, to maximize the species obtained, the plot was worked through from the outer to the inner part, thereby preventing ants from escaping the plot. Secondly, for the same reason, the plots were divided into smaller areas of 1 m² and these were worked through as fast as possible. Thirdly, everything which could be sifted was taken (leaf-litter, the surface of the humus layer, small twigs, wood pieces and roots). Fourthly, in contrast to the method described by B. Bestlmeyer in the accompanying book, instead of using ethanol, a wet 2 cm wide, folded leather ribbon was placed in the capture cup. This provided hiding-places for the animals and hence reduced fights and prevented desiccation. The method was well-suited for collecting ants since they were among the first arthropods that entered the capture cup. It also allowed the sorting of the ants to be performed efficiently because the ants could easily be caught with forceps as they ran out of the cup at

the time of inspection. Finally, after 24 hours of extraction, the sacks were emptied, sifted, the extract loosened and then refilled into the net. The cup was replaced by a new one and a second extraction performed over 24 hours.

Results

Taxonomic structure of the fauna

A total of 120 species was found, belonging to 49 genera. Five of the nine subfamilies occurring in the Indo-Australian region were found: Cerapachyinae, Dolichoderinae, Formicinae, Myrmicinae and Ponerinae (Table 1). Of the remaining four subfamilies, Aenictinae and Dorylinae are driver ants, the Pseudomyrmecinae are mainly plant-inhabiting ants and the Leptanillinae are mainly hypogaecic, and hence unlikely to be sampled in the litter.

Table 1. Taxonomic structure of leaf-litter inhabiting ants sampled in Pasoh Forest Reserve, Malaysia.

Subfamilies	Species	Genera
	Number /%	Number /%
Cerapachyinae	3 / 1.7	1 / 2
Ponerinae	32 / 26.7	16 / 32.7
Myrmicinae	70 / 58.3	22 / 44.9
Formicinae	13 / 10.8	8 / 16.3
Dolichoderinae	2 / 2.5	2 / 4
Total	120 / 100	49 / 100

The Myrmicinae were represented by 70 species and 22 genera. The two most species-rich genera were *Pheidole* and *Strumigenys*, followed by *Oligomyrmex* and *Tetramorium* (Table 2). The most frequent species found in each sampling area in terms of percentage frequency of capture, were Myrmicinae, including *Strumigenys uichancoi*, *Oligomyrmex* sp. and *Tetramorium* sp.

Table 2. The genera that were sampled, ranked by decreasing number of species.

Genus	Species	%	Genus	Species	%	Genus	Species	%
<i>Pheidole</i>	13	10.8	<i>Discothyrea</i>	2	1.67	<i>Harpegnathos</i>	1	0.83
<i>Strumigenys</i>	13	3	<i>Leptogenys</i>	2	1.67	<i>Lophomyrmex</i>	1	0.83
<i>Oligomyrmex</i>	6	10.8	<i>Ponera</i>	2	1.67	<i>Lordomyrma</i>	1	0.83
<i>Pachycondyla</i>	6	3	<i>Pseudolasius</i>	2	1.67	<i>Mayriella</i>	1	0.83
<i>Tetramorium</i>	6	5.0	<i>Pristomyrmex</i>	2	1.67	<i>Meranoplus</i>	1	0.83
<i>Crematogaster</i>	4	5.0	<i>Smithistruma</i>	2	1.67	<i>Myrmoteras</i>	1	0.83
<i>Hypoponera</i>	4	5.0	<i>Solenopsis</i>	2	1.67	<i>Mystrium</i>	1	0.83
<i>Monomorium</i>	4	3.33	<i>Acanthomyrmex</i>	1	0.83	<i>Odontomachus</i>	1	0.83
<i>Myrmecina</i>	4	3.33	<i>Amblyopone</i>	1	0.83	<i>Odontoponera</i>	1	0.83
<i>Acropyga</i>	3	3.33	<i>Anoplolepis</i>	1	0.83	<i>Pheidologeton</i>	1	0.83
<i>Cerapachys</i>	3	3.33	<i>Camponotus</i>	1	0.83	<i>Rhoptromyrmex</i>	1	0.83
<i>Gnamptogenys</i>	3	2.5	<i>Cardiocondyla</i>	1	0.83	<i>Rostromyrmex</i>	1	0.83
<i>Paratrechina</i>	3	2.5	<i>Diacamma</i>	1	0.83	<i>Polyrhachis</i>	1	0.83
<i>Vollenhovia</i>	3	2.5	<i>Dolichoderus</i>	1	0.83	<i>Proatta</i>	1	0.83
<i>Anochetus</i>	2	2.5	<i>Dysedrognathus</i>	1	0.83	<i>Probolomyrmex</i>	1	0.83
<i>Emeryopone</i>	2	2.5	<i>Echinopla</i>	1	0.83	<i>Technomyrmex</i>	1	0.83
<i>Cryptopone</i>	2	1.67						

The Ponerinae were represented by 32 species and 16 genera. The most species-rich ponerine genera were *Pachycondyla*, with six species, and *Hypoconera*, with four species.

The Formicinae were represented with 13 species and eight genera, the Dolichoderinae by two species and two genera and the Cerapachyinae by three species and one genus. The most species-rich genus of these three subfamilies was *Acropyga*, with three species.

It is obvious that the myrmicines, which contained 60% of the species sampled, are clearly predominant. Together with the ponerines, they constitute 85% of the species of leaf-litter and soil inhabiting ants in this region. Two genera were found for the first time in Pasoh: *Dysedrognathus* (Myrmicinae, Dacetoniini) and *Emeryopone* (sensu Bolton 1994) (Ponerinae, Ponerini).

Patterns in species richness

Considering that this investigation was not designed to be exhaustive, the actual number of soil and litter inhabiting ants in Pasoh can be expected to be even higher. The species frequency of

capture curve (Figure 2) shows a typical distribution for tropical regions, with many rare species and a small number of species with high abundance. This Figure shows the distribution for the three different plot sizes and all show the same trend. However, the columns for the smallest plot size (9 m²) show a distinct shift in the direction of the single captures. This large number of rare species suggests that there are many more species to be found.

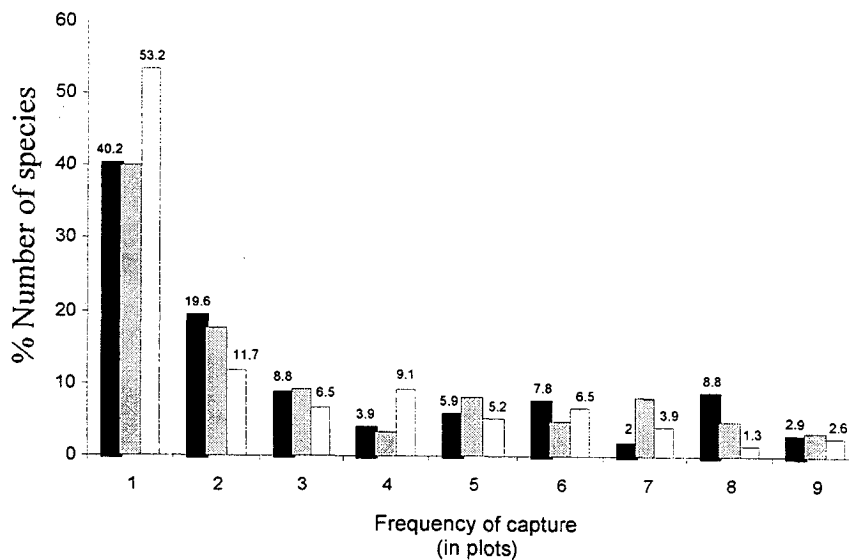


Figure 2. Frequency of capture for species in nine 9 m² = □, 16 m² = ▨, and 25 m² = ■ plots respectively.

This is confirmed by the species accumulation curves for each sample size, none of which shows a tendency to level out (Figure 3). Each curve gives a different prognosis of the species richness to be expected. This is an important consideration when comparing the results from different plot sizes; it is not possible to compare them directly.

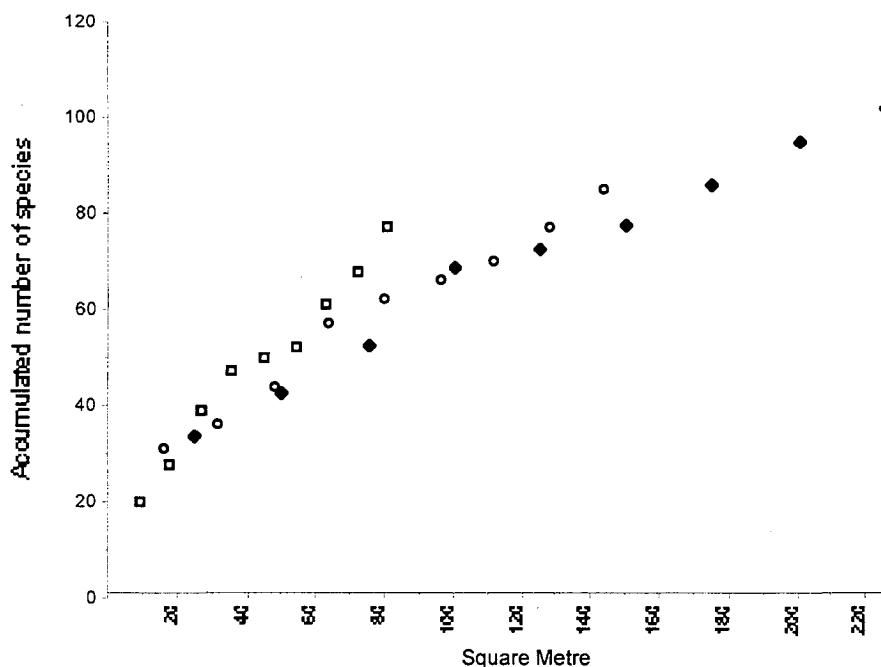


Figure 3. Species accumulation curves for the three plot sizes of 9 m² = □, 16 m² = ○, and 25 m² = ◆ respectively.

The histogram for frequency of capture of genera (Figure 4) shows a different pattern from the one for the frequency of capture of species (Figure 2). The frequencies of capture are more evenly distributed and much less biased toward the single captures. Furthermore, there is a slight increase for the most repeated captures of genera in comparison to the species captures.

The most frequently captured genera (in eight or nine plots) are myrmicines and ponerines, and they are also the ones with the largest number of species. The species within these genera are distributed such that each genus is represented in nearly all plots. Only rarely (10 out of 72) are more than 50% of the species of one genus found at one site.

There seems to be a pattern to how the species are distributed in the examined leaf-litter habitat. Three types of species distribution are found (Table 3), namely: 1) species within a genus that are either very frequently or very rarely found this applies to *Oligomyrmex*, *Pheidole*, *Strumigenys*, *Tetramorium*, *Monomorium* and *Hypoponera*; 2) species within a genus that were captured at a medium frequency or as single captures, but the genus had at least one species present in each plot and this applies to the species distribution

of *Myrmecina* and *Pachycondyla*; and 3) the remaining two most frequently collected genera, *Odontoponera* and *Odontomachus*, which were represented by only one species each and which were found in nearly every sample.

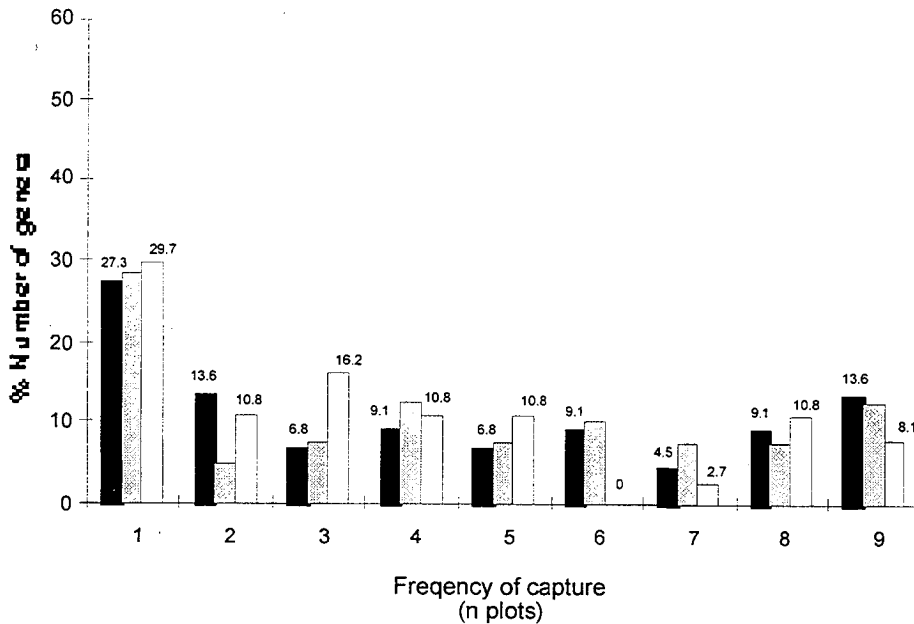


Figure 4. Frequency of capture of genera in nine 9 m² = □ ,16 m² = ▨, and 25 m² = ■ plots respectively.

Table 3. Frequency of capture for the most species-rich myrmicine and ponerine genera in largest plot size (25m²), (nine repeated captures = 100%, x = one species). The last column shows the mean number and standard deviation of species within each genus captured per plot.

Genus	Frequency of capture (n plots)									Mean spp. per plot
	P 1	P 2	P 3	P 4	P 5	P 6	P 7	P 8	P 9	
<i>Oligomyrmex</i>	x		xx						x	1.8±1.0
<i>Strumigenys</i>	xx	xxx	x				x	xx	x	4.6± 0.8
<i>Pheidole</i>	xxxxxx	xx		x				xx		3.3±1.3
<i>Tetramorium</i>		xx	x			x		x	x	3.0±0.7
<i>Monomorium</i>	x	x						xx		2.2±0.4
<i>Hypoponera</i>	xx	x					x			1.8±1.0
<i>Myrmecina</i>		x			x	x	x			1.3±0.8
<i>Pachycondyla</i>		xxxx		x			x			1.4 ±1.0
<i>Odontomachus</i>									x	0.9±0.3
<i>Odontoponera</i>									x	0.9± 0.3

Patterns in species density and turnover

Some interesting results for species density and turnover were revealed by applying the nested sampling area design. It indicated that plot sizes influenced the measurement of diversity.

Species density does not take abundance into account (see the chapter by J. Longino in the accompanying book). Table 4 lists the values of species density per m² for each 9 m² and 25 m² plot. On average, one more species was found on the 9 m² plots compared to the 25 m² plots.

Sorensen's similarity quotient was used to describe species turnover. The similarity-values of the 25 m² plots range from 37.5% to 63.8%, and those of the 9 m² plots from 28.5% to 66.7%. The mean values are 52.7% for the 25 m² plots and 43.0 % for 9 m² plots. These differences are highly significant ($P < 0.001$, Mann-Whitney U-Test). The higher species turnover in the 9 m² plots resulted from more single captures and a smaller number of repeated captures.

Table 4. Mean species density per m² for each area of the 25 m² and 9 m² plates. (A-25 = species density of 25 m², A-9 = species density of 9 m²).

Plots	A-25, per m ²	A-9, per m ²
P1	1.36	2.22
P2	1.16	2.44
P3	1.44	2.22
P4	1.64	2.22
P5	0.92	1.55
P6	1.24	2.00
P7	1.52	3.11
P8	1.76	3.22
P9	1.68	3.22
Mean	1.41	2.47

One of the important results of this analysis is that the sample area seems to have a substantial impact on the estimates of diversity. The sample area size therefore represents an important factor that must be taken into account in the interpretation of results. The sampling area design described here yielded manifold information and evaluation possibilities.

In particular, the separate calculations for three different plot sizes enable us to make more detailed comparisons within and between diversity studies.

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Chapter 4 - Ant inventories along elevational gradients in tropical wet forests in Eastern Madagascar

Brian L. Fisher

Introduction

Inventory methods designed to permit rapid, replicable, and quantitative sampling of the leaf litter ant fauna were used to investigate altitudinal and latitudinal patterns in ant diversity in wet tropical forests in eastern Madagascar. A total of 14 inventories were conducted at four regional sites. I discuss the nature of leaf litter ant assemblages in Madagascar and present summary information on species richness, species accumulation curves, and species turnover. Detailed discussions of the species collected, their relative abundance, faunal similarity, species turnover, and the efficacy of inventory methods are presented in Fisher (1996a, 1998, 1999a).

Methods

Study sites

Elevational gradients were surveyed at four localities in eastern Madagascar (Figure 1):

- (1) Réserve Naturelle Intégrale (RNI) d'Andohahela. 24°33'–34'S, 46°48' - 49'E; elevational sites surveyed: 400, 800, and 1250 m.
- (2) RNI d'Andringitra, 22°12'–14'S, 46°58'– 47°01'E; elevational sites surveyed: 785, 825, 1275, and 1680 m.
- (3) Western Masoala Peninsula, 15°34'–41'S, 49°57'–50°00'E; elevational sites surveyed: 25, 425, and 800 m.
- (4) Réserve Spéciale (RS) d'Anjanaharibe-Sud, 14°45'S, 49°26'–30'E; elevational sites surveyed: 875, 1200, 1565, and 1985 m.

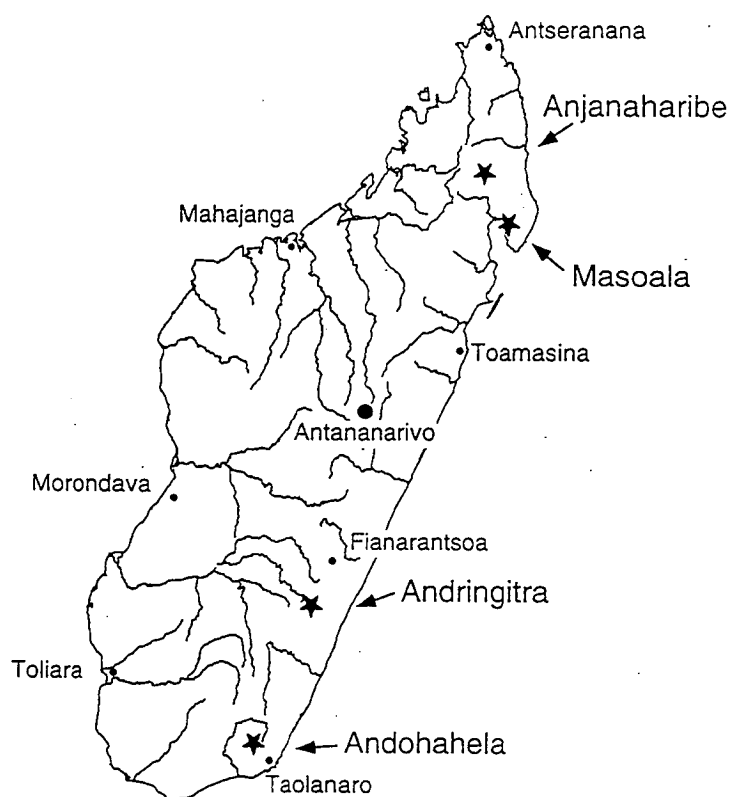


Figure 1. Inventory sites in eastern Madagascar: Réserve Naturelle Intégrale (RNI) d'Andohahela, RNI d'Andringitra, Western Masoala Peninsula, Réserve Spéciale d'Anjanaharibe-Sud.

At each elevational site, the survey method used 50 pitfalls and 50 leaf litter samples (Winkler), in parallel lines 10 m apart, along a 250 m transect. Pitfall traps were placed and leaf litter samples gathered every 5 m along the transect. Further details are found in Fisher (1996a, 1998, 1999a, and J. Delabie et al. in the accompanying book).

Data analysis

Only records of ant workers were used in data analysis. To assess the completeness of the survey for the elevations sampled, I plotted cumulative species per sample curves for each elevation. Species accumulation was plotted as a function of the number of leaf litter and pitfall trap samples taken. For the analysis, each leaf litter sample was paired with the

adjacent pitfall sample, collectively termed a *station sample*. Species-accumulation curves for the 50 stations per transect, as well as incidence-based coverage estimator (ICE) and first-order jackknife estimates of the total number of species in the local community from which the samples were taken, are plotted for each succeeding station sample. Detailed descriptions of these methods of analysis are found in Fisher (1996a, 1998, 1999a, 1999b) and J. Delabie et in the accompanying book.

Complementarity (the distinctness or dissimilarity) of the ant assemblages (sensu Colwell and Coddington 1994) at different elevations was assessed using an index of species turnover. Beta-diversity (species turnover between elevations) was calculated using beta-2 developed by Harrison et al. (1992): $\text{beta-2} = (S/a_{\text{max}}) - 1$, where S = the total number of species in the two elevations combined, and a_{max} = the maximum value of alpha-diversity (i.e., number of species) among the elevations compared.

Results and Discussion

From all sampling methods, I collected and identified 128,677 ants comprising 36 genera and 471 species. These included 2032 queens and 780 males. Leaf litter and pitfall methods yielded 117,044 worker ants belonging to 30 genera and 381 species. The relative prevalence of the different subfamilies in the leaf litter and pitfall samples is shown in Table 1. The fauna is dominated by the Myrmicinae, followed by the Ponerinae. The 8 most dominant ant genera comprised 77% of the species in leaf litter and pitfall samples (Table 2).

Table 1. The total number and percentage of species per subfamily based on worker ants collected from pitfall and leaf litter samples in the four localities.

Subfamily	Total species	%
Myrmicinae	234	62.4
Ponerinae	93	24.4
Formicinae	30	7.9
Cerapachyinae	18	4.7
Dolichoderinae	3	0.8
Pseudomyrmecinae	3	0.8

Table 2. The eight dominant ant genera, representing 80% (304 species) of all species collected from pitfall and leaf litter samples in the four localities.

Genus	Total Species	%
<i>Pheidole</i>	68	17.8
<i>Strumigenys</i>	51	13.4
<i>Tetramorium</i>	51	13.4
<i>Hypoponera</i>	50	13.1
<i>Monomorium</i>	36	9.4
<i>Camponotus</i>	21	5.5
<i>Cerapachys</i>	18	4.7
<i>Crematogaster</i>	9	2.4
<i>Leptogenys</i>	9	2.4
<i>Paratrechina</i>	8	2.1
<i>Discothyrea</i>	6	1.6
<i>Proceratium</i>	6	1.6
<i>Madamorium</i>	5	1.3
<i>Smithistruma</i>	5	1.3
<i>Amblyopone</i>	5	1.3
<i>Pachycondyla</i>	5	1.3
<i>Prionopelta</i>	5	1.3
<i>Oligomyrmex</i>	4	1.0
<i>Mystrium</i>	4	1.0
<i>Technomyrmex</i>	3	0.8
<i>Tetraponera</i>	3	0.8
<i>Plagiolepis</i>	1	0.3
<i>Aphaenogaster</i>	1	0.3
<i>Eutetramorium</i>	1	0.3
<i>Kyidris</i>	1	0.3
<i>Leptothorax</i>	1	0.3
<i>Pilotrochus</i>	1	0.3
<i>Anochetus</i>	1	0.3
<i>Odontomachus</i>	1	0.3
<i>Platythyrea</i>	1	0.3
Total	381	

Because of its long isolation from other land masses, the level of endemism of ant species on Madagascar is high. For the island, 90% of the valid specific and subspecific ant taxa are endemic (Fisher 1996b, 1997). For the relatively undisturbed wet forest localities surveyed, endemism is close to 100% (Fisher 1996a, 1998, 1999a). The ant fauna of Madagascar, however, is incompletely known, with two-thirds of the 1000 estimated species

on the island thought to be undescribed (Fisher 1997). As an extreme example, of the 51 species of *Strumigenys* collected in the four localities (Table 2), 50 are undescribed.

Species accumulation curves demonstrate the efficacy of the leaf litter and pitfall methods in sampling the majority of the ants in the leaf litter (Fisher 1999b). Species accumulation curves for observed, ICE, and jackknife estimates showed a decrease in the rate of species accumulation, but were still increasing slowly. For example, accumulation curves for the 825 m site on the Masoala Peninsula, the most species rich site, are presented in Figure 2 (for plots of other elevations and localities, see Fisher 1996a, 1998, 1999a). These curves indicate that within the area of the survey, the technique employed collected the majority of ants foraging and living in the leaf litter in the area encompassed by the 250 m transect, and that with increased sampling effort using the same methods (i.e., adding more pitfall and litter stations) in the same area, only marginal increases in species richness would be attained. Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely collect additional species. Nevertheless, these results show that the inventory techniques used in this study provide sufficient sampling for statistical estimation and comparison of species richness, and comparison of faunal similarity and species turnover.

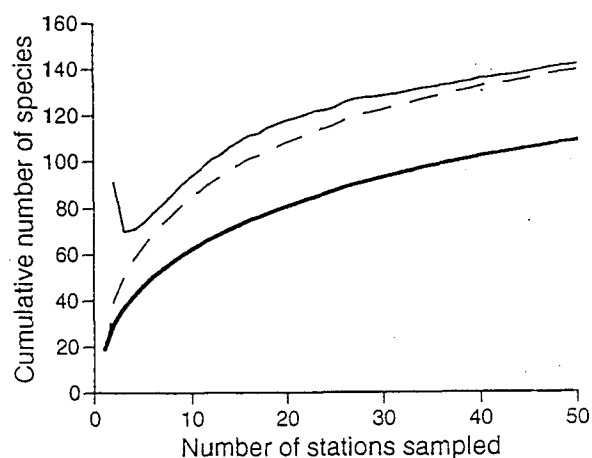


Figure 2. Assessment of leaf litter ant sampling technique for the most species rich site: 825 m on the Masoala Peninsula. The lower species accumulation curve (thick line) plots the observed number of species as a function of the number of stations sampled. The upper curves display the non-parametric first order jackknife (dashed line) and the incidence-based coverage estimator, ICE (solid line), estimated total species richness based on successively larger numbers of samples from the data set. Curves are plotted from the means of 100 randomizations of sample accumulation order.

An alternative approach to evaluating the efficacy of the sampling methods in terms of completeness of sampling (i.e., accumulation curves), would be to ask what minimum number of collections would be necessary to provide the same relative ranking of species richness among elevations as shown in Figure 3. Do pitfall samples alone show the same mid-elevation peak? Not at all localities. For example, within the Masoala Peninsula locality, the 825 m site had the lowest number of species recorded from pitfalls. Species accumulation curves for pitfall samples are still rising rapidly after 50 samples, which suggests that pitfall samples in this study do not provide sufficient sampling for comparison among elevations. It is also possible that pitfalls sample a different subset of the ant fauna, which may not show a mid-elevation peak. In tropical dry forest sites, the pitfall trap method collects a greater number of individuals and species (Fisher and Razafimandimby 1997). For mini-Winkler samples, the same relative ranking in observed species richness was reached and maintained after 25 samples. A smaller number of leaf litter samples will produce a more incomplete species list necessary for complementarity studies, but fewer samples may be appropriate for addressing questions on patterns of species richness.

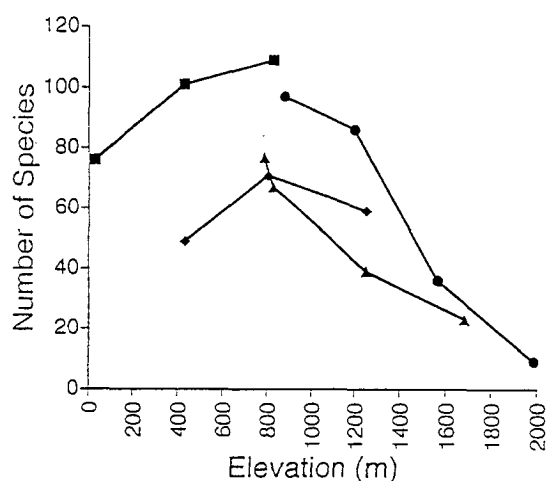


Figure 3. The number of ant species as a function of elevation. Data are from pitfall and mini-Winkler samples from the RNI d'Andohahela (F), the RNI d'Andringitra (H), the Masoala Peninsula (B), and the RS d'Anjanaharibe-Sud (J).

Species richness did not decrease monotonically as a function of elevation. Species richness peaked at mid-elevations (Figure 3). Along an elevational gradient, the peak in species richness at mid-elevations is thought to be the result of the mixing of two distinct,

lower and montane forest assemblages (see below; Fisher 1998). After the mid-elevation peak, species richness declined rapidly, reaching a minimum of nine species at 1985 m. This rapid decrease in species richness probably reflects climatic variables, mainly the reduction of radiant energy (Brown 1973; Fisher 1996a) and resultant decreasing primary productivity (Rosenzweig and Abramsky 1993). For ants in montane forests, the most important factor regulating colony survival may be clouds and high humidity which prevent bright sunlight from raising the ground temperature toward the optimal level for larval development and for worker foraging activities.

Faunal similarity and beta-diversity measures suggest a division of the ant fauna into two communities, one occurring in lowland forests ≤ 875 m and the other in montane forests ≥ 1200 m. For example, species turnover calculated using beta-2 was greatest at mid-elevation (Figure 4). Similar patterns were found using the Jaccard and Morisita Indices (Fisher 1996a, 1998, 1999a).

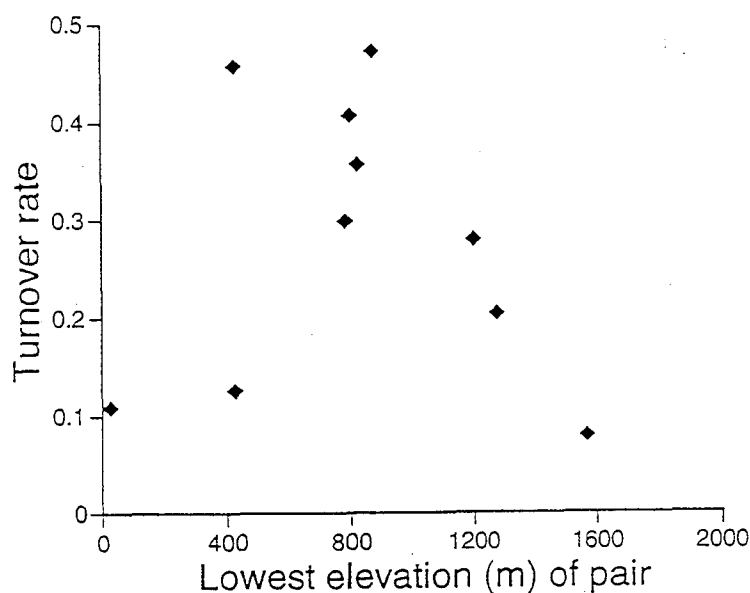


Figure 4. Species turnover rate between adjacent elevational sites along the gradient calculated using the Beta-2 Index of Harrison et al. (1992). Adjacent elevations are separated by approximately 400 m. The lowest elevation in the comparison is plotted. Data are from pitfall and mini-Winkler samples from all localities.

Conclusions

These studies demonstrate that effective methods to inventory hyperdiverse groups like ants are possible, and that results from inventories can make important contributions towards understanding landscape-level patterns of invertebrate biodiversity. In addition, the specimens collected in ant inventories in Madagascar are invaluable for future studies of the systematics, evolution, and biogeography of Malagasy ants.

By comparison with data on other biotic groups, these inventories will permit the analysis of how species composition and diversity change with altitude and latitude. These comparative data are important for understanding intertaxon differences in diversity patterns, which should be factors critical for developing a conservation strategy based on diversity.

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Chapter 5 - The Australian rain forest ant fauna: A biogeographic overview

Alan N. Andersen and Jonathan D. Majer

Introduction

Despite being the most arid of habitable continents, Australia has a substantial rain forest estate (Figure 1). Humid rain forest occurs throughout the eastern seaboard, from northern Queensland to Tasmania, where rainfall is high throughout the year (Webb and Tracey 1981). Extensive tracts of tropical and temperate rainforest occur in northern Queensland and Tasmania respectively, but the remainder exists as intermittent patches within a predominantly sclerophyll landscape dominated by *Eucalyptus*. Throughout the seasonal (monsoonal) tropics of northwestern Australia, rainforest occurs as thousands of small patches within a savanna matrix, and is normally restricted to areas of permanent water or topographic positions offering shelter from fire (McKenzie 1991; Russell-Smith 1991).

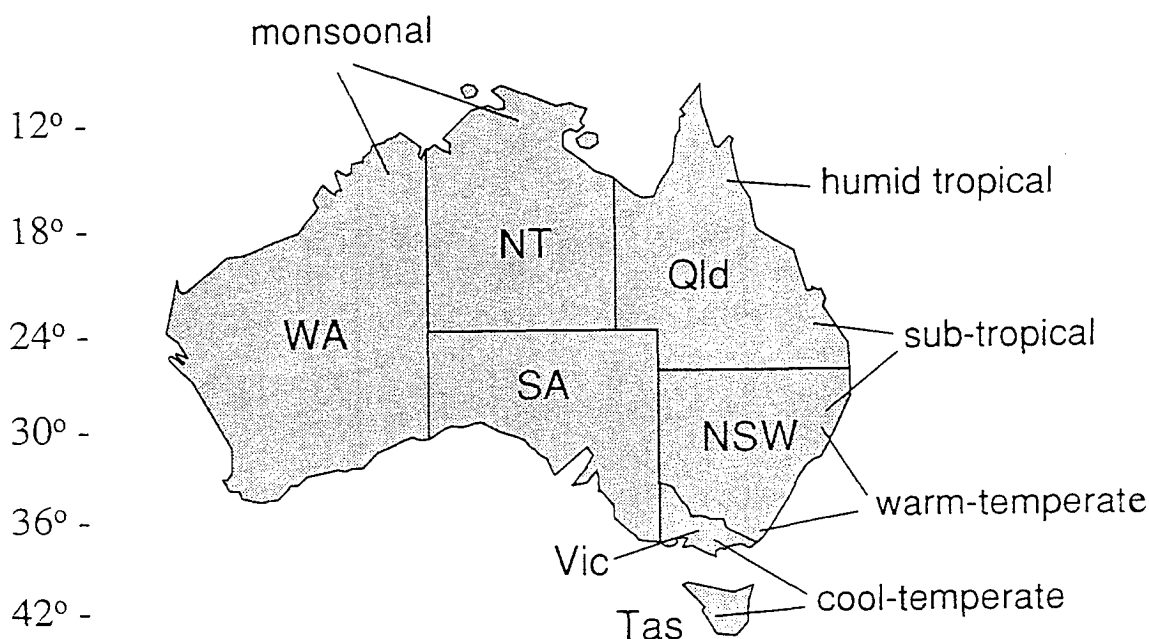


Figure 1. Location of major rain forest types in Australia.

McKenzie (1991) has reviewed the origins of Australian rain forests and noted that they contain both Gondwanan and Laurasian elements. Throughout most of the Tertiary, Australia is believed to have been covered by rain forest primarily of Gondwanan origin, following separation from the Antarctic continent. Indomalayan elements began colonizing Australia from the early Tertiary onwards, thus enriching floristic composition. Climatic variability and increasing aridity over the past 20 million years has caused these rain forests to contract to relictual patches, being replaced by more open and xeromorphic vegetation. Some of the more extensive tracts of rain forest in northeastern Queensland are thought to have resulted from expansions of relictual forests during the current relatively warm and wet interglacial conditions, and some may only be a few thousand years old.

Rainforest ant faunas

By Australian standards, the rain forest ant fauna is relatively low in diversity and well-known taxonomically. Paradoxically, there is a paucity of quantitative information on ant species composition, in contrast to the strong tradition of ant survey and community ecology in sclerophyll habitats (Andersen 1995). Extensive ant surveys of monsoonal rain forest patches have recently been conducted in both the Kimberley and NT, but there have only been a handful of surveys in rainforest anywhere in eastern Australia (Table 1). Faunistic information is therefore both inconsistent and incomplete, which severely constrains the analysis we present here.

Tropical rain forests

The rainforest ant fauna of northeastern Queensland is remarkably disjunct from the exceptionally rich, arid-adapted fauna of adjacent savanna (sclerophyll) habitats. The savanna fauna is dominated by distinctly Australian taxa, such as species of *Iridomyrmex*, *Melophorus*, *Meranoplus* and *Monomorium*, and is similar to that of the central arid zone (Greenslade 1979; Andersen 1993). In contrast, Queensland's humid rainforests support ant

Table 1. Summary list of quantitative surveys of Australian rain forest ants (see Figure 1 for locations of biogeographic zones). Rain forest sites have also been included in general ant surveys of the Kakadu region of the NT (Greenslade 1985) and the Cooloola - Noosa region of southern Qld (Greenslade and Thompson 1981), but with insufficient detail reported to be included here.

Biogeographic Zone	Location	Methodology	References
Monsoonal tropics	Kimberley, W.A.	comprehensive sampling from 16 sites	Andersen and Majer 1991; Andersen 1992
	Northern N.T.	comprehensive sampling from 7 sites, pitfalls and hand collections only from 45 sites	Andersen and Reichel 1994; Reichel and Andersen 1996
Humid tropics	Atherton Tableland, Qld	pitfalls, Winklers and baiting at two undisturbed and three cleared sites	J. King et al. 1998
Sub-tropics	nil		
Warm temperate	East Gippsland, Vic	pitfall traps only at two sites	Andersen 1983
Cool-temperate	Wilson's Promontory, Vic	pitfall traps only at a single site	Andersen 1986
	Tasmania	comprehensive sampling at 12 sites, and miscellaneous collections from other sites	Greenslade 1991

faunas composed primarily of Indomalayan elements (Taylor 1972). Many genera, including *CalRYPTOMYRMEX*, *Echinopla*, *Gnamptogenys*, *Myrmecina*, *Pristomyrmex*, *Proceratium* and *Rhopalothrix*, occur in Australia only in these rainforests, and represent southerly extensions of the far richer rain forest faunas of the Indomalayan region (Taylor and Brown 1985). Species endemism is low - for example, most of the 106 species known from Iron Range in far northern Queensland also occur in New Guinea (Taylor 1972), but increases with latitude.

Tropical rain forests feature numerous arboreal taxa, such as *Oecophylla* and species of *Crematogaster*, *Polyrhachis*, *Tetraponera* and *Podomyrma* (Taylor and Brown 1985). This contrasts with sclerophyll habitats, where arboreal taxa are poorly represented, and the ants foraging on vegetation are primarily ground-nesting species (Majer 1990; Andersen and Yen 1992).

Many of the Indomalayan rain forest taxa also occur in rain forest patches in monsoonal northwestern Australia, with their representation decreasing with longitude (distance from Queensland) and, more dramatically, latitude (decreasing rainfall). Almost all these species also occur in Queensland, with only a few known to be locally endemic, and only one (a species of *Crematogaster*) known from South-East Asia but not Queensland (Reichel and Andersen 1996). The most common ants in rain forest patches throughout the monsoonal region are unspecialized species of *Monomorium*, *Pheidole*, *Tetramorium* and *Paratrechina* (Andersen and Majer 1991; Reichel and Andersen 1996). In drier patches, the canopy is often broken and dominated by deciduous species, resulting in incursions by arid-adapted taxa such as species of *Iridomyrmex* and *Melophorus* (Andersen and Majer 1991; Reichel and Andersen 1996).

Patch species richness in the Northern Territory (18-60 - Reichel and Andersen 1996) is generally similar to the Kimberley (19-41; Andersen and Majer 1991), but the Northern Territory has many more specialist rain forest taxa (27% vs 9% of total species) and more arboreal species (13% vs 5%). This reflects the generally higher rainfall of the Northern Territory, and its closer proximity to Queensland (Reichel and Andersen 1996). Despite these differences, functional group composition of the Kimberley and Northern Territory faunas is almost identical (Table 2). The limited data that are available suggest that functional group composition of humid Queensland rainforests is very similar to that in monsoonal northwestern Australia, except for a relatively poorer representation of Subordinate Camponotini (primarily species of *Camponotus* and *Polyrhachis*), and greater prevalence of cryptic species (Table 2).

Temperate rain forests

With increasing latitude, the incidence of Indomalayan taxa, arboreal species and Generalized myrmicines (species of *Pheidole*, *Crematogaster* and parts of *Monomorium*) all decrease, and cold-adapted Gondwanan elements become increasingly prevalent (Table 3, Figure 2). Similar patterns also occur with increasing altitude. In cool-temperate rainforests of Victoria and Tasmania, Indomalayan taxa, arboreal species, Generalized myrmicines and Opportunists are

all largely absent, and the most common ants are Gondwanan taxa (such as *Prolasius*, some groups of *Monomorium*, *Notoncus* and *Myrmecorhynchus*), and cryptic species (primarily species of *Solenopsis* and *Hypoponera*). Unlike the situation in the tropics, there is not a major discontinuity in the ant faunas of cool-temperate rainforest and sclerophyll habitats. Indeed, virtually all ant species of cool-temperate rainforests also occur in surrounding wet sclerophyll forests.

Table 2. Functional group composition (percentage of total species) of rainforest patches in the Kimberley region of Western Australia (16 sites), the Northern Territory (52 sites) and on the Atherton Tableland in northern Queensland (two undisturbed sites only). References are given in Table 1.

Functional group	Kimberley	Northern Territory	Atherton
Dominant Dolichoderinae	9	4	3
Subordinate Camponotini	18	20	8
Climate Specialists:			
Hot	9	7	3
Tropical	5	8	8
Cryptic species	13	10	24
Opportunists	15	22	22
Generalized Myrmicinae	22	21	19
Specialist Predators	7	9	8

Table 3. Functional group composition (percentage of total species) of tropical and temperate rainforests of eastern Australia. References are given in Table 1.

Functional group	Tropical (Atherton)	Warm- temperate	Cool- temperate (Victoria)	Cool- temperate (Tasmania)
Dominant Dolichoderinae	3	14	10	13
Subordinate Camponotini	8	0	0	4
Climate Specialists:				
Hot	3	0	0	0
Tropical	8	0	0	0
Cold	0	14	70	58
Cryptic species	24	28	20	21
Opportunists	22	14	0	0
Generalized Myrmicinae	19	28	0	0
Specialist Predators	8	0	0	4

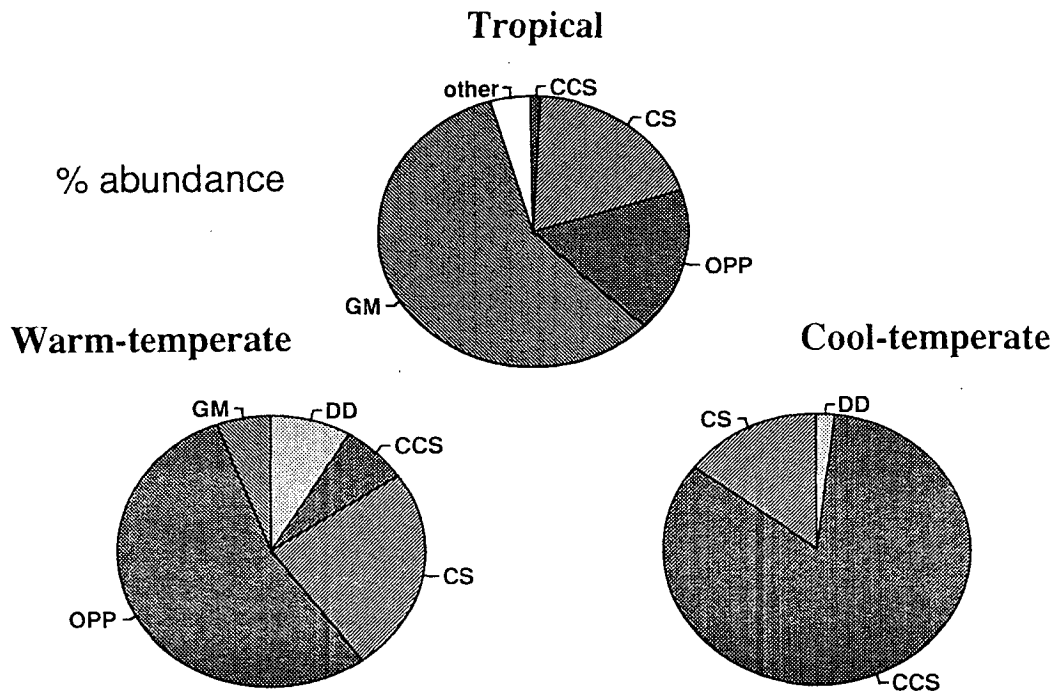


Figure 2. Relative abundances of functional groups in tropical (King et al. 1998), warm-temperate (Andersen 1983) and cool-temperate (Andersen 1986) rain forests.

Conclusion

Australia, the most arid of habitable continents, has a noteworthy estate of rain forest ants, featuring Indomalayan elements in the tropical north, and Gondwanan elements in the cool-temperate south. Overall functional group composition of rain forest faunas appears to be similar throughout the tropics, but the incidence of Indomalayan taxa decreases from the humid to monsoonal zones. The most striking feature is the low diversity of rain forest faunas in the humid lowland tropics, which contrasts starkly with the high diversity of adjacent sclerophyll habitats, and the extraordinary diversity of lowland tropical rain forests elsewhere in the world, including nearby New Guinea (Wilson 1959). This presumably reflects the marked climatic fluctuations experienced by Australian rain forests over recent geological time, suffering severe contractions during glacial periods.

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Chapter 6 - Ground ant communities from central Amazonia forest fragments

Heraldo L. Vasconcelos and Jacques H.C. Delabie

Introduction

The purpose of this study was to determine the effects of forest fragmentation on the ant community inhabiting the soil and litter of an Amazonian forest. Deforestation and forest fragmentation are thought to be important processes contributing to present day high rates of species extinction (Myers 1988), although data on the magnitude of these effects on forest invertebrates are still scanty. In addition to this purpose, we here evaluated the efficiency of three sampling methods to estimate ant species richness and characterize the ant fauna of the fragments. The study was conducted as part of the Biological Dynamics of Forest Fragments Project (Bierregaard et al. 1992), a long-term collaborative project between the National Institute for Research in the Amazon (INPA) and the Smithsonian Institution.

Methods

Study areas

The study sites were located in three nearby cattle ranches (hereby referred to as Dimona, Esteio and Porto Alegre), approximately 80 km north of Manaus, Brazil (2°21'S, 59°50'W), where between 1979 and 1984 a series of forest fragments (generally square in shape) of 1, 10 and 100 ha were isolated from surrounding forest by clearing the intervening vegetation to establish cattle pastures. Between September 1993 and January 1994, we collected ants in three 1-ha fragments (one in each ranch), in three 10-ha fragments (also one per ranch), in two 100-ha fragments (one at Dimona and one at Porto Alegre) and in one continuous forest area (BDFFP reserve 1301 at Esteio).

In each of these 9 areas a 1-ha plot was delimited and, within this, a total of 36 sampling points, distributed at intervals of 20 m, was established. Whenever possible, these plots were located in the center of the fragment. This was not possible in one 10-ha fragment (at Dimona), as it was dissected by a small creek in its center. Since we only sampled in plateau areas (so as to avoid possible confounding effects of topography on ant community structure), the plot in this fragment was established at the edge of the fragment. The plot in the only continuous forest site studied was located 500 m distant from the edge between the forest and the cleared area, the same distance used to place our sampling plots in the 100-ha fragments. For the purpose of the statistical analyses, we considered this to be a "fragment" of 10,000 ha.

Ant sampling

At each sampling point, we installed a pitfall trap that operated continuously for 48 h. Traps consisted of a plastic cup (6.5 cm of diameter) partially filled with a 5% aqueous solution of liquid soap. In addition, at each sampling point we collected a sample of leaf-litter and a sample of soil. All litter in a 70 x 70 cm quadrat was collected and placed in a plastic bag. Ants were then extracted manually from the sample by sorting the litter over a white tray. A similar procedure was used to extract ants from the soil samples. Samples of soil, removed from an area of 25 x 25 cm to a depth of 25 cm, were sieved in a wire sieve (0.8 cm mesh) before extracting the associated ants.

For each sampling point, we recorded the number of ant species collected in the pitfall trap, in the litter, in the soil, as well as the number of species collected using all three methods combined. To estimate the total number of ant species that could potentially be found in each fragment we used the method of sequential progressive sampling (Lauga and Joachim 1987), which is calculated by the formula:

$$S=s1.s2.(p - 1)/(s1.p) - s2$$

where S is the estimated number of species, s_1 is the average number of species per sample, s_2 the total number of species in all samples and p is the number of samples.

Data analysis

Differences in ant species richness, species diversity and evenness between different sized forest fragments were analyzed by Analysis of Covariance, using fragment size (log transformed) as the covariate and location of the fragment (ranch) as a random factor. Ant species richness was measured as the number of species collected per hectare (hereafter "point" species richness). We used the indices of Shannon H' and E (Brower and Zar 1977) to respectively measure ant species diversity and evenness.

As an index of similarity between fragments in terms of ant species composition, we used the ordination scores produced by non-metric multidimensional scaling (NMDS; Gauch 1982), for an ordination with a two-dimension solution which used chord distance as the association measure.

Results

A total of 227 ant species, representing 60 genera and 8 subfamilies, were recorded (Appendix 1). Of these genera, the most speciose was *Pheidole* with 49 species, followed by *Gnamptogenys*, *Pachycondyla*, *Crematogaster*, *Trachymyrmex*, *Paratrechina* and *Hypoponera* with between 7 and 11 species each.

Of the three methods employed to collect ants, litter sampling was the most efficient in terms of the number of species collected. The mean number of species collected per fragment was significantly greater in the litter than in the pitfall traps and soil, whereas the number of species collected in the pitfall traps was greater than in the soil (ANOVA, $F_{2,16} = 29.87$, $p < 0.001$; Table 1). Although the number of species recorded per fragment was greater in the litter samples than in the pitfall traps, the total number of species recorded by each of these two methods in all the nine fragments studied was quite similar; and both yielded greater numbers than collections from the soil samples (Table 1). Litter sampling was also the best

method to predict overall ant species richness (number of species collected using the three methods combined) in the fragments, as indicated by its greater regression coefficient (r^2) value, a measure of fit between two variables. The regression coefficient between number of species in the litter and the total number of species was 0.77 ($n = 9$), whereas the corresponding value for pitfall traps was 0.56 and for soil was 0.46.

Table 1. Number of ant species (total, number unique, number per subfamily and mean number per fragment) collected using three different sampling methods in forest fragments near Manaus, Brazil.

Subfamily	Litter samples	Pitfall traps	Soil samples
Myrmicinae	96	82	53
Ponerinae	33	36	33
Formicinae	11	12	12
Dolichoderinae	3	5	0
Ecitoninae	1	5	1
Cerapachyinae	2	0	5
Pseudomyrmecinae	1	2	0
Leptanilloidinae	0	0	2
Total (unique)	147 (43)	142 (39)	106 (20)
Mean \pm SD	54.2 \pm 11.6	45.7 \pm 7.9	30.3 \pm 5.6

The number of species that were unique to each method ranged from 20 to 43 species, a number which usually represented more than 20% of all species collected by that method (Table 1). This indicates that these methods are complementary to each other. Their use in combination, therefore, better characterized the ant fauna of the fragments. Species of Cerapachyinae, for instance, were almost only recorded in the soil samples, whereas those in the Ecitoninae were mostly recorded in the pitfall traps. On the other hand, many Myrmicinae were only recorded in the litter samples (Table 1).

Table 2 shows the observed relationship between fragment area and "point" species richness. Overall, the number of ant species per ha was not significantly different between fragments of different size ($F_{1,3} = 1.06$, $p = 0.38$). However, there was a marginally significant interaction between the effects of fragment area and fragment location on point species

richness ($F_{2,3} = 7.91$, $p = 0.06$). At both Dimona and Esteio, species richness tended to increase with fragment area, whereas at Porto Alegre it tended to decrease (Table 2).

Table 2. Variations in species diversity between different sized fragments of forest near Manaus, Brazil.

Ranch	Fragment size (ha)	Total no. Species, observed (and estimated)	Species diversity (H')	Species evenness (E)	No. species in pitfall traps	No. species in litter samples	No. Species in soil samples
Esteio	1	80 (106)	3.78	0.86	40	45	26
	10	91 (124)	3.98	0.88	39	54	26
	>10,000	109 (151)	4.30	0.92	58	61	44
Dimona	1	94 (129)	4.09	0.90	45	59	29
	10	99 (139)	4.23	0.92	42	67	29
	100	111 (149)	4.28	0.91	52	73	34
P.Alegre	1	98 (140)	4.10	0.89	55	48	28
	10	78 (117)	3.86	0.89	34	41	29
	100	79 (112)	3.87	0.89	46	40	28

This trend is observed with the number of ant species recorded using all three collecting methods combined, and generally also for each method individually. The one exception was of the soil samples, from which we recorded the same number of species in the different sized fragments at Porto Alegre (Table 2).

Ant species diversity, as calculated by the Shannon index (Table 2), also did not differ significantly between fragments of different size ($F_{1,3} = 1.99$, $p = 0.25$), but here again there was a significant interaction between fragment size and fragment location ($F_{2,3} = 9.5$, $p = 0.05$). Evenness in species distribution within the fragments (as calculated by the Shannon index of evenness) tended to increase as fragment area increased ($F_{1,3} = 6.26$, $p = 0.09$; Table 2), and no significant interaction with fragment location was found for the evenness index ($F_{2,3} = 3.87$, $p = 0.15$).

Ant species composition was affected by both fragment area and fragment location. This was shown by the significant relationship between the scores produced by the first axis of the ordination analysis (NMDS) with fragment area ($F_{1,3} = 21.33$, $p = 0.02$) and fragment location ($F_{2,3} = 13.72$, $p = 0.03$; Figure 1); there being no interaction between these two factors ($F_{2,3} = 0.60$, $p = 0.60$). NMDS scores for the second axis of the ordination analysis were not affected by fragment area and location ($p > 0.20$ in both cases).

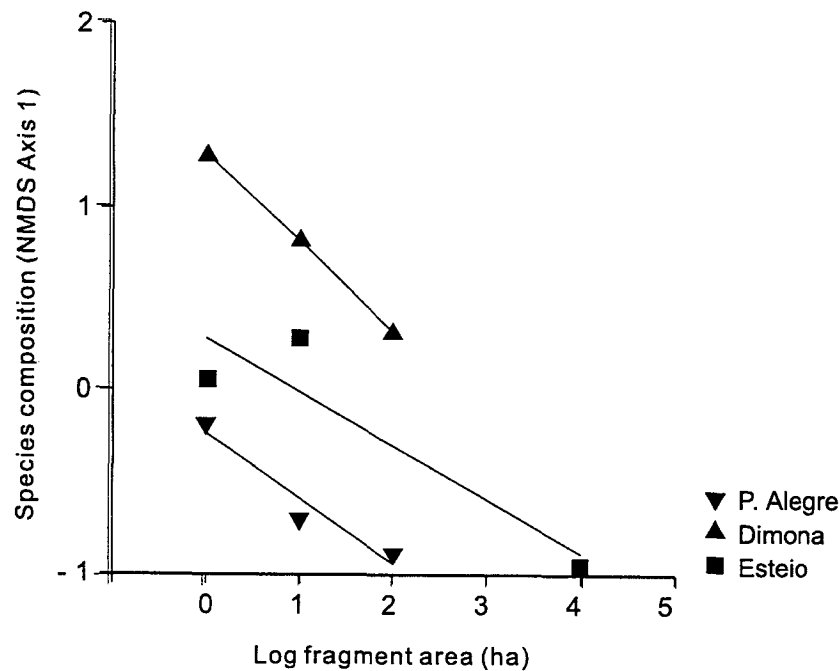


Figure 1. Relationship between fragment area and ant species composition (represented by the ordination scores produced by non-metric multidimensional scaling) in forest fragments from three localities near Manaus, Brazil.

Discussion

Effects on species richness and composition

The results presented here strongly suggest that forest fragmentation affects the structure of ground-living ant communities. "Point" species richness tended to vary according to the area of the fragment and although in some of the sites species richness increased, in others it

decreased; there was always a difference of 20% or more in the number of species found in the smallest as compared with the largest fragment sampled within each of those sites. Furthermore, in all of these three sites we found significant effect of fragment area on ant species composition.

In addition to increasing the chances of local extinctions by reducing population sizes, one of the consequences of forest isolation is that wind and light penetrates the periphery of the fragment, changing its microclimate and vegetation structure. This edge-effect (Lovejoy et al. 1986) tends to decrease as distance from the border of the fragment increases, thus producing a proportionally greater effect on the smaller fragments (Malcolm 1994). Some forest ant species are not tolerant of high temperatures (Torres 1984) and thus may not occur near the periphery of the fragments where conditions are warmer (Kapos 1989). Changes in vegetation structure near to forest edges may have produced a similar effect. For instance, *Astrocaryum sociale*, a stemless palm characteristic of the understorey of central Amazonian forests, is less common near the edge of forest fragments than in the forest interior (Wandelli 1991). Due to characteristics of its morphology, this palm acts as a litter trap, funneling leaves and small branches from the overstorey directly to the palm root zone. This creates a favourable microhabitat for forest ants, and more ants are found in the litter accumulated near the roots of *A. sociale* than in the litter found on the adjacent soil (Vasconcelos 1990). If some of these ants are mostly, or exclusively, found in this type of microhabitat, then a reduction in the abundance of *A. sociale* due to forest isolation will cause a concomitant change in ant species richness and composition. Possibly, such relations also exist with other plants that have been reduced near edges. Litter depth increases near to forest edges, and variations in litter depth have been found to explain part of the variation in ant species composition along forest edges (Carvalho and Vasconcelos 1999). Finally, changes in ant species composition and diversity in the fragments may have been caused through invasion of species from nearby human-managed habitats. Studies of forest ant communities in Japan (Terayama and Murata 1990) show that as the area of a forest fragment is reduced, more forest ant species are lost and the fragment becomes more susceptible to invasion by species from nearby disturbed habitats.

Effects of surrounding vegetation

The observed interaction between the effects of fragment area and fragment location on point species richness is intriguing and deserves further investigation. Given the lack of pre-isolation data, we can not exclude the possibility that our results simply reflect some inherent variability in ant species richness between the fragments studied. However, there were differences in the history of isolation between fragments located in different sites and this may have accounted, at least in part, for the observed differences in the relationship between fragment area and ant species richness across these sites. The area around the fragments at Dimona and Esteio was burned and used as pasture for 2-7 years before being abandoned, whereas that around the fragments at Porto Alegre was not burned, nor was it used as pasture, being abandoned immediately after clearing of mature forest. As a result, forest regrowth and the recovery of the original forest ant community was faster around the fragments at Porto Alegre than around those of the other sites (Vasconcelos 1999). This suggests that ant species richness in small Amazonian forest fragments is dependent upon the structure and composition of the vegetation surrounding these fragments, and that the closer the similarity between this vegetation and forest vegetation, the greater the richness in ant species in the fragments. In support of this view are the findings of Webb (1989), who studied the invertebrate fauna of fragmented heathland in Britain. There, it was found that where more structurally diverse vegetation surrounds a piece of heathland, there is a tendency for a greater richness of invertebrates to be recorded on the heathland.

Geographical variation in species composition

The similarity in ant species composition was generally greater for fragments located within the same site (ranch) than between fragments located in different sites, regardless of fragment size (Figure 1). Whether this represents, as seems to be the case for leaf-litter beetles (Didham et al. 1998), an effect of forest fragmentation rather than of geographical variation in species composition (gamma diversity *sensu* Cody 1986), remains to be determined. However, studies in other localities indicate that distance does indeed affect ant species

composition. Wilson (1958) recorded the occurrence of distinct shifts of ant species composition over distances of only a few kilometers in relatively continuous, homogeneous rain forest in New Guinea, whereas Majer (1983) showed that the similarity of the ant fauna in forests of western Australia decreases with increased distances. These results must, thus, be taken into account in studies that use ants as indicators of environmental change. From a point of view of conserving Amazonian biodiversity, this seemingly spatial autocorrelation in ant species composition has important implications. It indicates that forest reserves should be large enough to compensate for discontinuities in species distributions, and that representative areas should be maintained as reserves in different geographic locations of Amazonia.

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Appendix 1. Number of species within different ant genera collected in forest fragments near Manaus, Brazil.

Genera	Esteio			Dimona			Porto Alegre		
	1ha	10h a	>10.000 ha	1ha	10ha	100 ha	1ha	10ha	100 ha
PONERINAE									
<i>Amblyopone</i>	0	1	2	1	0	0	0	0	0
<i>Anochetus</i>	3	3	2	3	2	4	3	1	2
<i>Centromyrmex</i>	0	0	0	0	0	1	0	0	0
<i>Discothyrea</i>	1	0	0	0	1	1	1	0	1
<i>Ectatomma</i>	2	2	2	2	2	2	1	2	1
<i>Gnamptogenys</i>	3	3	3	4	4	3	4	4	3
<i>Heteroponera</i>	0	0	0	0	1	0	0	0	0
<i>Hypoponera</i>	7	6	7	7	6	7	6	7	6
<i>Leptogenys</i>	1	1	0	2	0	0	2	2	1
<i>Odontomachus</i>	2	1	2	4	2	3	1	3	2
<i>Pachycondyla</i>	4	6	8	3	6	6	7	8	6
<i>Platythyrea</i>	0	0	0	0	1	0	0	0	0
<i>Prionopelta</i>	1	1	1	1	1	1	1	1	1
<i>Thyphlomymex</i>	1	2	2	1	1	2	1	2	2
CERAPACHYINAE									
<i>Acanthostichus</i>	0	2	1	0	1	1	1	0	0
<i>Cerapachys</i>	0	0	1	0	1	1	0	1	0
<i>Sphinctomyrmex</i>	0	0	0	1	0	0	0	0	0
ECITONINAE									
<i>Eciton</i>	0	1	0	0	0	0	0	1	0
<i>Labidus</i>	0	0	0	0	0	1	0	0	0
<i>Neivamyrmex</i>	1	2	3	1	0	0	0	0	0
LEPTANILLOIDINAE									
<i>Asphinctanilloides</i>	0	1	1	0	0	0	0	0	0
MYRMICINAE									
<i>Apterostigma</i>	1	1	1	3	1	1	3	1	0
<i>Atta</i>	0	0	0	0	0	1	0	0	0
<i>Blepharidatta</i>	1	1	0	1	1	1	1	1	1
<i>Carebara</i>	0	1	0	0	0	0	1	0	0
<i>Cephalotes</i>	1	0	0	0	0	0	0	0	0
<i>Crematogaster</i>	3	4	6	5	5	3	3	5	3
<i>Cyphomyrmex</i>	3	2	2	2	2	2	2	1	1
<i>Daceton</i>	0	1	0	0	0	0	0	0	0
<i>Erebomyrma</i>	0	1	1	1	1	0	1	1	1
<i>Glamyromyrmex</i>	0	0	1	0	0	1	2	1	0
<i>Gymnomyrmex</i>	0	0	0	1	0	0	0	0	0
<i>Hylomyrma</i>	0	0	0	1	0	1	1	0	0
<i>Lachnomyrmex</i>	0	0	0	1	0	0	0	1	0
<i>Leptothorax</i>	0	0	0	1	1	0	0	0	0
<i>Megalomyrmex</i>	1	3	3	3	3	4	3	1	1
<i>Myocepus</i>	0	1	1	0	0	0	0	0	0
<i>Myrmicocrypta</i>	2	1	2	1	1	2	1	0	2
<i>Neostruma</i>	0	0	0	0	0	2	0	0	0
<i>Ochetomyrmex</i>	1	2	2	2	2	2	2	0	1
<i>Octostruma</i>	0	1	1	0	0	1	0	0	0
<i>Oxyepoecus</i>	0	1	1	0	0	1	0	0	0
<i>Pheidole</i>	25	25	28	22	22	26	23	16	22
<i>Rogeria</i>	1	1	1	2	4	2	2	2	2
<i>Sericomyrmex</i>	1	1	2	2	2	2	0	1	1
<i>Solenopsis</i>	5	3	5	3	5	5	3	3	4
<i>Strumigenys</i>	0	0	2	1	2	2	1	1	2
<i>Talaridris</i>	0	0	0	1	0	0	0	0	0
<i>Trachymyrmex</i>	3	2	5	1	4	5	4	5	4
<i>Tranopelta</i>	0	0	0	0	0	0	0	1	1
<i>Wasmannia</i>	1	1	1	1	0	1	2	1	0
FORMICINAE									
<i>Acropyga</i>	0	1	2	0	1	3	2	0	3
<i>Brachymyrmex</i>	0	1	0	1	2	1	1	0	1
<i>Camponotus</i>	1	0	2	1	2	1	4	1	0
<i>Paratrechina</i>	3	4	5	4	6	6	4	3	4
DOLICHODERINAE									
<i>Azteca</i>	0	0	0	0	1	0	2	0	0
<i>Dolichoderus</i>	0	0	0	2	1	1	1	0	0
<i>Dorymyrmex</i>	0	0	0	0	0	1	0	0	0
<i>Linepithema</i>	0	0	0	0	0	0	1	0	0
PSEUDOMYRMECINAE									
<i>Pseudomyrmex</i>	1	0	0	1	1	0	0	0	0

Chapter 7 - Minesite rehabilitation studies: A method for visualizing succession

Jonathan Majer

Introduction

Ants have frequently been used as indicators of the success of minesite rehabilitation. One of the challenges of this approach has been to track the succession of the ant community through time, while taking into account the varying rehabilitation procedures which have evolved over this period. Swaine and Greig-Smith (1980) note that the use of ordination to analyse repeated enumerations of the same plots over a period of time has been investigated by a number of authors. For instance, Austin (1977) used this technique to look at changing plant species composition in a lawn, van der Maarel (1969) undertook a similar approach with dune grassland and Hopkins (1968) investigated seasonal change in a tropical savanna. On the aquatic side, Williamson (1963) looked at annual changes in marine plankton and Allen and Skagen (1973) looked at short-term changes in freshwater algae.

The approach has met with varying degrees of success since the successional changes can be of a lower magnitude than existing spatial gradients in the data, thus resulting in confusing spatial and temporal trends. Swaine and Greig-Smith (1980) overcame this problem by first eliminating the effect of initial differences between stands and then subjecting the data to principal components analysis.

Examples

We have recently analysed the annual collections of ant species from three rehabilitated bauxite mines and one forest control (Majer and Nichols 1998). Samples have been collected from 1976, prior to initial revegetation, through to 1989. Application of an ordination technique has been extremely helpful in observing the temporal trends and also the ways in which the ant community responds to different rehabilitation treatments. Interpretation of the trends has been relatively easy as the

ant communities all had similar starting points ie. zero species and no vegetation.

With the difficulty in obtaining long-term funding, it is seldom possible to follow a successional pattern over a long period of time. An alternative 'chronosequence' approach is to select a range of sites which represent known times after disturbance and then sample them all at the same time. The resulting differences are then taken to be representative of different stages in the successional process. This technique can be fraught with problems because the chosen sites may not represent areas which originally possessed identical communities. Thus attempts to detect trends in the chronosequence of sites may be confounded by inherent differences in community composition. This is not such a problem with minesite rehabilitation studies since the sites tend to have similar characteristics and the rehabilitation procedures are often standardised between sites or, if they are not, they have probably been documented.

Two overseas studies with which I have been involved illustrate the application of this approach. Bauxite is being mined at Poços de Caldas in the state of Minas Gerais, Brazil. The native vegetation of the area is a patchwork of subtropical rain forest (mata) and grassy woodland (campo). The company is attempting to rehabilitate the area to mata by returning the topsoil and revegetating the area with mata plant species. Application of an ordination procedure to ant data from rehabilitated plots ranging from 1 to 10 years old and also from a mata and a campo control suggests that the ant fauna in the younger plots is not developing towards that of the mata ant community (Figure 1). Furthermore, application of minimum spanning-tree analysis to the points on the ordination indicates that the fauna in the younger plots has more in common with that of the campo than of the mata (Figure 1). Only in the oldest two plots, where the tree canopy has closed up, is the fauna more allied to the mata than to the campo.

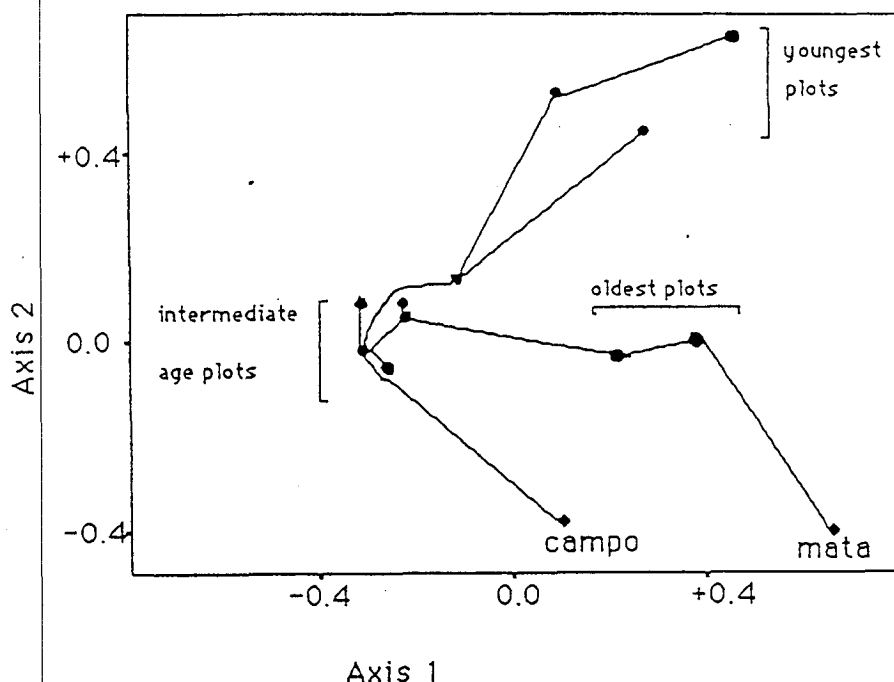


Figure 1. Separation of control and rehabilitated plots at Poços de Caldas, Brasil derived by the use of principal co-ordinates analysis of ant species presence/absence data using Sorensen's similarity quotient. The lines were derived by minimum spanning-tree analysis and connect plots which have the most similar ant fauna (adapted from Majer 1992).

The second example comes from Richards Bay, South Africa, where a mosaic of cleared and pristine coastal dune rain forest is being mined for mineral sand. The company is attempting to rehabilitate much of the area to coastal dune rain forest by revegetating the area with forest species and also with those plants which characterise the succession which occurs when shifting cultivation-type farms are abandoned. Application of an ordination-type procedure to the ant data from plots ranging from 0.3 to 13 years old and to three forest controls indicates that the first part of the succession is not "directed" towards the original forest community. Only in the older plots does the ant community start to resemble that of the original forest (Figure 2). Consideration of temporal changes in the physical and biological components of the environment suggests that this dichotomy in the direction of the succession is mediated by the presence of the pan tropical ant species, *Pheidole megacephala*,

which progressively attains massive densities in the youngest rehabilitation and declines to negligible levels from the 6-year old through to 13-year-old rehabilitation (Majer and de Kock 1992).

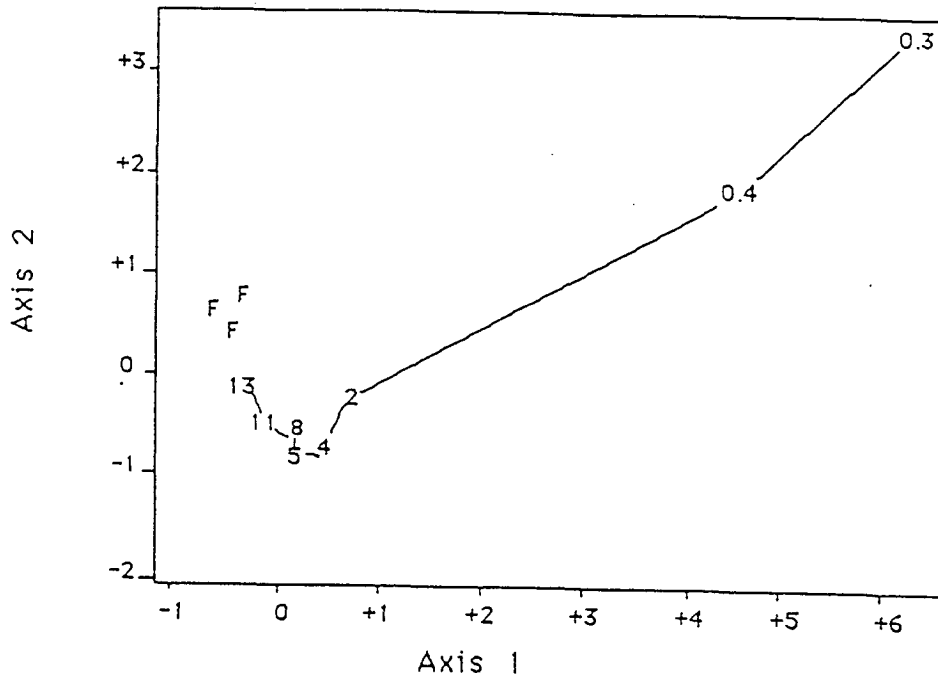


Figure 2. Separation of control and rehabilitated plots at Richards Bay, South Africa, derived by the use of correspondence analysis on ant species presence/absence data. Numbers represent the age, in years, of the rehabilitation and 'F' represents the forest controls. The lines have been drawn in to indicate the path of the succession (adapted from Majer and de Kock 1992).

I have found the various ordination-type procedures to be very useful in understanding the temporal variation in often complex data sets. Provided that users take steps to account for site differences and design their sampling programs so that the trends are not confounded by seasonal effects, this is a particularly useful method for visualising successional processes.

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The cover illustration was drawn by Nicolette Layover and depicts the soil-dwelling ant *Melophorus majeri* Agosti, an unusual member of this genus, that has only been found at two heathland localities in the extreme south of Western Australia.